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CANOPY GAP REGENERATION AND DYNAMICS IN THE AFROMONTANE FOREST OF BALE MOUNTAINS

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Abstract

Change in forest communities and recruitment of new individuals into tree populations depend on the dynamics and formation of canopy gaps. Gap dynamics and canopy gap regeneration were investigated in Harena Forest of Bale Mountains, Southeastern Ethiopia at altitudes ranging from 3000 – 2000 m a.s.l. Wind was found to be the main type of natural disturbance resulting in the overthrow and snapping of heavily crowned emergent canopy trees. The most affected canopy species by this disturbance regime was ***Dombeya torrida***. 14 species were found to be gap makers. The mean DBH of the gap makers was 50.4cm. Mean gap size of the forest was (289.74$\pm$165.48 m^2) and almost all the gaps were found in sloppy areas. Twenty-four different woody species were encountered as gap–filler species along different altitudes. Of these species, six were recruited only in gap sites while the gap environment favored most of the rest. Seedling and sapling density of the gaps were higher than that of closed canopied sites indicating the importance of gaps for maintaining woody species diversity in the forest. The strong negative correlation between slope, altitude, and species and seedling densities indicates that both factors affect gap regeneration. Otherwise, gap size differentiation in the forest and replacement probabilities in the Harena forest was weak (less than 0.5) except for ***Diospyros abyssinica(0.86)***; most of the gap makers were replaced by other sub-canopy species of the forest. Thus, species recruitments in gaps of the forest are likely due to chance effects. Germination trial of the soil seed banks of Harena forest collected from the sampled gaps and canopied sites has revealed a high dominance of herbaceous species. Only five of the 24-gap filling species and three of the gap maker species were recovered in the soil seed bank of the gap sites and even that was in smaller density. Thus, the chance of getting an immediate replacement of the canopy trees, if removed naturally, was found to be minimal.

Key words: Canopy regeneration, Disturbance, Gap regeneration, Gap makers, Gap filler species, Replacement probabilities, soil seed Bank.

1 INTRODUCTION

Forest ecosystems are of great global, regional and local ecological role. Apart from ecological aspect, forests are also of significant importance for the economies of many tropical and sub tropical countries. However, enormous population size of these nations caused over exploitation and over utilization of the forest resources for different purposes such as timber, fuel and food. This increasing and intensive destruction of forest ecosystems results in a rapid decline in variety at ecosystem level, an increase in species extinction as well as a reduction of genetic variation within several species.

Ethiopia was once covered with extensive natural forests. According to NAE (1981), the land area covered with forest was estimated to be not less than 30%. Surprisingly enough, the country was rich floristically due to the wide range of climatic, altitudinal and vegetation influences it exhibited. As a result, Ethiopia comprises most of the major ecological systems and also possesses one of the largest and most diversified indigenous tree species in Africa.

Ethiopia, among others, consists of the afro-montane area, which was once largely covered with evergreen forests. Unfortunately, only a fragment of this remains and even this is at constant risk of destruction (Demel Teketay and Gransterom, 1995). The main factors in the degradation of the moist evergreen montane forest ecosystem are related to human activities. These factors are mainly timber extraction, coffee plantations, agricultural expansion, and settlement and deliberate or accidental fire hazards. Besides the national efforts being undertaken, most of the forest stands continued to be deforested or severely degraded in quality and quantity because of the irresponsible activities of humans.

The Harena state forest is one of the largest remnants of moist afro-montane rain forest in southern part of the Bale Administrative Zone. Different researchers have described different aspects of this human activity impacted forest ecosystem at different times. For instance, Friis (1992) has described the vegetation zone, Bussmann (1997) made phytosociological study, Lisanework Negatu and Mesfin Tadesse (1989) made a detailed ecological study, Geetachew

Tesfaye *et al*. (2002), studied the regeneration of 14 economically important tree species and Getachew Tesfaye *et al*. (2004) studied soil seed bank regeneration after the 2000 fire impact.

It is believed that forest ecosystems are not static. They change in structure and composition. Runkle (1982) and Obiri and Lawes (2004) believe that plant communities change as individuals die and are replaced. The ways in which communities die and are replaced might not be the same for all communities. Therefore, how deaths and replacements occur in time and space has an impact on many aspects of forest community structure and composition (Abayneh Derero *et al*., 2003). The recruitment of new individuals into tree populations and the consequent dynamics and abundance of tree species mainly depend upon the dynamics of canopy gap formation. Hence, gaps are usually considered to be the most important for regeneration and dynamics of forest ecosystems (Runkle, 1981; 82; Auguspurger, 1984; Lui and Hytteborn, 1991; Midgley, 1993; Ostertag, 1998).

The death, windfall and branch breakage of a single or a group of trees causes natural gap dynamics. Canopy gap formation is brought about by different disturbance factors which cause changes in growing space either by eliminating or altering the total amount of growing space available to plants (Oliver and Larson, 1990).

The presence or absence of a species within a gap habitat depends on the local growth of the population and the net migration of individuals into and out of the area (Ricklefs, 1990). This variation in temporal and spatial patterns of species recruitment within canopy gaps may be due in part to variations in shade and tolerance (Auguspurger, 1984).

On the other hand, the nature of the soil seed bank is also an important condition that plays a significant role in the self-maintenance of the forest. According to Grime (1979), vegetation frequently recovers very rapidly after surface disturbance as a result of germination of seed bank.

Therefore, in Harena forest where there is great human impact on the ecosystem, understanding the nature of gap dynamics and regeneration will be of paramount importance for its conservation.

2 LITERATURE REVIEW

2.1 Gap Dynamics and Regeneration

2.1.1 Gap dynamics and its importance

Gap dynamics is a basic natural mechanism for self-maintenance of different forest ecosystems, developed over the course of many tree regenerations in the absence of catastrophic external influences. It is associated with the mortality of individual old trees, causing openings to appear in the canopy letting in light and giving smaller trees the possibility to grow and assume a place in a stand. Hence, gaps are usually considered as vital areas for regeneration, dynamics and diversity of various types of forest ecosystems. In the past, a number of researchers have studied and described the importance of gaps in different forest types. For instance, Runkle (1981; 1982); Popma & Bongers (1988); Yemamoto (1989); Brokaw (1985b); Abayneh Derero ***et al***. (2003) have described the importance of gap dynamics in mesic forest in the Eastern United States, tropical rain forest in Mexico, nemoral ***Fagus*** forest in Japan, humid tropical forest and dry afro-montane forest in Ethiopia respectively.

Forest ecosystems with gap dynamics have a large accumulation of dead wood on the ground, and of dead organic matter in the soil (Vitousek and Denslow, 1986). According to Bongers and Popma (1988), the occurrence of a gap causes abrupt changes in the forest structure and the availability of resources to the plants. In gaps, special soil profiles are formed as a result of the continuous falling of old trees along with their root systems. Therefore, gap formation is followed by changes in microenvironments of the forest, especially isolation on forest floors. Roberts and Gilliams (1995) have suggested that soil nutrient resources typically are assumed to change following gap formation, usually with nutrient availability increasing initially and subsequently decreasing through later stages of succession. Oliver and Larson (1990) have also indicated that the availability of water, nutrient and oxygen changes following gap formation. Thus, the special ecological conditions under the canopy, high degree of light, moisture and variety of substrates, provide forest ecosystems with a diverse plant community. According to

Lui and Hytteborn (1991), the spatial and temporal heterogeneity in regeneration opportunities induced by gaps in the forest canopy is critical to the dynamics of many forest communities.

2.1.2 Gap origin

A gap is part of a forest stand where one or more trees (or limbs) have created an empty space in the canopy either through death or through death and sub sequent felling, and where regenerating tree species have not reached more than 2/3 of the average canopy tree height (Runkle, 1981; Lui and Hytteborn, 1991). According to Kint *et al*., (2004), gap origin is linked to minor disturbance events which cause the death and toppling of trees through the forest. In other words, a gap can exist only in a matrix of mature trees, with a recognizable more or less continuous border consisting of trees. The tree, which creates gap, is said to be gap maker (Obiri and Lawes, 2004). Various factors such as fungal and insect attacks and/or wind or fire contribute to the death of gap makers. On the other hand, the mode of mortality of gap makers varies among tree species. For instance according to Putz *et al*. (1983), wood properties in a tropical forest are most important in determining the mode of death.

2.1.3 Disturbance and its roles

2.1.3.1 What is disturbance?

“A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment (White and Pickett, 1985). Numerous tropical and temperate forest studies suggest that small disturbances that produce canopy openings are important for population dynamics of forest trees and to forest composition, structure and heterogeneity (Runkle, 1982; Brokaw, 1985b; Taylor *et al*., 1996; Abayneh Derero et al., 2003). Natural disturbance at various scales is also needed in order to maintain tree species diversity (Yemamoto *et al*., 1995). Furthermore, disturbances are powerful ecological factors that determine the spatial, size and age distributions of plant population (Van der Maarel, 1993). Thus, all forest ecosystems undergo a cycle of disturbance and regeneration. Disturbances increase spatial and temporal heterogeneity of light, temperature moisture, nutrient regimes and seedbeds and create mosaics of sites that favor the regeneration of different species and lead to patchy forest structures (Taylor ***et al***., 1996). The variation in the distribution of gap sizes, the composition of species and size of seedlings or saplings in forest ecosystem indicates that disturbances never favor equally the regeneration of all tree species (Yemamoto ***et al***., 1995). Hence, the disturbance regime to which a forest is subject is important for its composition and structure. In many forest ecosystems, gap-regenerating forests may not be in compositional equilibrium due to climatic changes. Lertzman (1995) suggested that this non-equilibrium status could make a substantial contribution to species co-existence over long term.

2.1.3.2 Disturbance and its magnitude

Disturbances can be characterized by their spatial extent time involved and magnitude. According to Van der Maarel (1993), spatially limited and low intensity disturbances lead to patch dynamics while high intensity and large-scale disturbances lead to regeneration succession. It is believed that patch dynamics may allow a competitively inferior species to co-exist within a land escape dominated by a competitively superior species by providing temporary refugia from competition and or releasing resources formerly taken by a competitively dominant species Following the cessation of the disturbance, the dominant species recovers and invades the gap eventually eliminating the gap species. Watt (1947) believes that disturbance leads to regeneration succession if the species invading the gap successfully regenerates within the gap and continues to occupy the gap.

2.1.3.3 Factors affecting disturbance

The sensitivity of forest trees to disturbance factors is characteristic of species. On the other hand, the timing and sequence of disturbance are critical factors in determining stand and landscape scale vegetation patterns (Veblen ***e***t ***al***., 1992). Disturbance results in environmental heterogeneity that favors the maintenance of some flexibility in the expression of regeneration traits (Houle, 1994). According to Stewart *et al*. (1991) and Kint *et al*. (2004), Community response to disturbance varies widely and depends on the types severity size and frequency of disturbance and species life history attributes such as dispersal ability, shade tolerance, growth rates, longevity and seed bed requirements. In short, disturbances are the main source for the variations that are observed between pathways in stand development.

2.1.3.4 Variables affecting gap regeneration

The effect of canopy gap on the environment and vegetation inside or near it depends on characteristics of the gap, of which the most important is gap size (Bongers and Popma, 1988). Gaps vary in shape and size. These variations as have been suggested by Hunter and parker (1993), are the products of the mechanism of gap formation and the tree species involved in the process. The gap size distribution depends upon the distribution between single and multiple tree fall gaps. Gap size is mainly responsible for variation of light intensity, which plays a major role in forest regeneration. According to Dirzo *et al*. (1992), the influence of gap size on light environment is important in understanding the dynamics of communities. In his study, Williams (1992) found that gap size affects both survivorship and performance of gap colonists via competitive interactions and the effects of gap microclimate. He further suggested that gap size affects both species richness and the nature of seedling populations. Canopy gap size can play a major role in determining composition of tree regeneration after disturbance (Runkle, 1982 and Wright *et al.*, 1998). In other words, species response to canopy gaps varies. Limited dispersal leads species to require relatively large gaps and or gaps that remain open for relatively long periods. This factor may prevent the evolution of other gap species (Philip, 1995). Some species may survive and become established in fairly small gaps. Kufer and Runkle (1996) have indicated that gap composition is closely linked to site conditions, including slope, soil conditions and site location. Runkle (1981) also found that with increased gap size, vegetation within gaps increased in woody species diversity, total basal area and total number of stems, where stems also showed accelerated growth into larger size classes.

On the other hand within single tree gaps, light conditions are optimal for the advanced regeneration of seedlings established prior to gap formation that grows rapidly without the risk of massive regeneration of competing species (Kint *et al*., 2004). The species composition of the regeneration phases is largely determined by the size of the gaps where as the regeneration of light demanding species is expected to occur in big gaps (Lui and Hytteborn, 1991).

2.2 Soil Seed Bank and Gap Regeneration

2.2.1 Importance and distribution of soil seed banks

Soil seed banks play an important role in determining plant communities after disturbance, and they partly reflect the history of vegetation and contribute to its future (Demel Teketay, 1996). Soil seed banks vary in spatial and horizontal distributions. For instance, vertical investigation of soil layer in tropical rainforest indicated that the greatest diversity is found in the upper soil layer (Demel Teketay and Gransterom, 1995;Getachew Tesfaye *et al*., 2004).

Information on soil bank characteristics such as species number, quality and depth distribution can provide an estimate of the regeneration potential after disturbance. Gap dependent species for the establishment of seedlings in gaps do have the habit of forming a short-term persistent seed bank. Many seeds show patchy distributions in the soil and thus species could be missed by sampling soil cores (Bakker *et al*., 1996).

2.2.2 Advanced regeneration

According to Ricklefts (1977), in mature tropical forests where gaps arise mainly as a result of windfall, the most important forms of regeneration are those involving vegetation sprouts, banks of seedlings originating from fruits dispersed by animals, and more rarely, wind dispersed seed. Many of the species produce seeds intermittently over a long life history and rate of successful regeneration are exceedingly low. Therefore, these species in a mature forest depend for successful regeneration upon advance regeneration.

2.2.3 Soil seed banks versus plant life forms

Most tree species have relatively large seeds and poor long distance dispersal. According to Grime (1979), large seed banks are particularly characteristics of shrubs and perennial herbs occurring in habitats subjected to intermittent disturbances. Therefore, the fact that most of the dominant tree species do not accumulate seeds in the soil suggests that their regenerating from seed would be unlikely if mature individuals disappeared. In a similar way, species with extremely small seeds have an obligatory light requirement. Demel Teketay and Gransterom (1995) found that many of the herbs seem to recruit after minor disturbances such as single tree wind fall, grazing and soil disturbance in afro- montane forests. In their study Rico-Gray and Garcia (1992) have also found that species consisting the original woody structure of the mature forest are rare or absent due to the lack of seed sources and failure of dispersal, lack of dispersal agents or long distance. According to them, herb species were the most important life forms in the soil seed banks.

Johnson (1975) on his part has found that the lack of viable buried seeds provides a partial explanation for the slow vegetation recovery observed. The species that were growing in older stands seemed to produce seeds that did not survive in the soil for any length of time. In his work, the annuals were found to appear significantly in fields after cultivation

Seeds of certain species may germinate only inside a gap as is the case in many pioneer species. Plants never regenerate outside their habitat (Vazquez-yanes and Orozco-Segovia, 1984; cited in Bongers and Popma, 1988). This will be a major determinant of its ecological amplitude and geographical distribution. Regeneration from banks of persistent buried seeds in shrubs and trees, for example, is restricted to species which are associated with frequently disturbed vegetation (Grime, 1979). In a similar way, seeds of certain species may germinate only inside a gap, as is the case in many pioneer species (Vazquez -yanes &Orozco -Segovia, 1984; cited in Bongers and Popma, 1988).

2.2.4 Factors influencing regeneration from seed banks

Several factors may contribute to the limitation of regenerative activity of plant species. One of these is predation by animals and fungal attacks In his study on seed demography of *Acer species*, Tanaka (1995) has shown that the predation pressure on viable seeds was high, for the low germination rate of the released viable seeds he encountered. Effects of predation by animals are likely to be particularly important in mature forests where regeneration often depends upon the maintenance of a bank of slow growing seedlings and saplings. In a similar way, grazing of vegetation by animals has significant effect on regeneration potential in gaps. Several studies have shown this. For instance, the grazing treatment experiment by McDonald *et al*. (1996) has indicated that a number of seeds in the deeper horizon than not grazed treatments, possibly due to trampling of the soil by the hooves of the animals. Demel Teketay and Gransterom (1995) have also found that grazing has potential role in incorporating seeds into the soil. On the other hand, up ward movement of seeds by certain invertebrates in effecting regeneration was documented. For instance, earthworms bring viable seeds to the soil surface and play, therefore, a role in plant recruitment (McDonald *et al*., 1996).

3 OBJECTIVES

3.1 General Objective

- To investigate canopy gap regeneration and dynamics in Harena Afromontane forest, Bale Mountains

3.2 Specific Objectives

- To identify gap filling species and document their richness across different gap sizes and altitudes.
- To identify modes of disturbance and relate them to gap filling species
- To find out any niche- partitioning by gap fillers
- To evaluate the probability of self replacement of canopy tree species in gaps by comparing gap filling species with surrounding canopy species as well as with those germinated from soil seed bank

4 MATERIALS AND METHODS

4.1 Description of the Study Site

4.1.1 Location

The Bale mountains massif, which is located on the eastern part of the Great Rift Valley, constitutes the largest proportion of the south eastern high lands of Ethiopia as well as that of the north east tropical Africa (Miehe and Miehe, 1994). On the southern slopes of the mountains, the Harena escarpment forms a sharp transition zone to the hot savanna areas of the southern parts of Ethiopia (Bussman, 1997).

The study was conducted in Harena afro-montane forest (39^0 and 40^0 E and latitudes 6^0 $20^{'}$ and 6^0 $50^{'}$ N) of Bale Mountains (Fig. 1). The Harena forest covers an area of about 7000 km^2 (Getachew Tesfaye *et al.*, 2002) and represents one of the largest remaining relatively intact natural forests of Ethiopia. Its altitude varies from 3800 m asl to 1500 m asl whereby there is a noticeable sharp drop in slopes from 3800 - 2800m, moderate drops from 2800-2300 and then followed by a ± gentle slopes (Lisanework Negatu and Mesfin Tadesse, 1989). Furthermore, Harena forest is known for being the catchments area of various rivers and streams such as Shawe and Geremba that are tributaries of Welmel River that drains into Genale River.

4.1.2 Geology

The soils of Bale Mountains are of volcanic origin resulting from the Oligocene eruptions of the Terrapean lava (Mohr, 1963). The rocks of the study area were found to contain trachytes with rhocytes, basalts agglomerates and tuffs where weathering of the basalt and trachytes formed mainly red or red brown to black silty loam (Weinert and Mazurele, 1984). In Bale Mountains, recent glaciations and other forms of erosion have modified the original topography of the mountains following tectonic uplift (Lisanework Negatu and Mesfin Tadesse, 1989). Therefore, the substrate of the Harena escarpment is believed to be the out come of the decomposition of the volcanic materials.

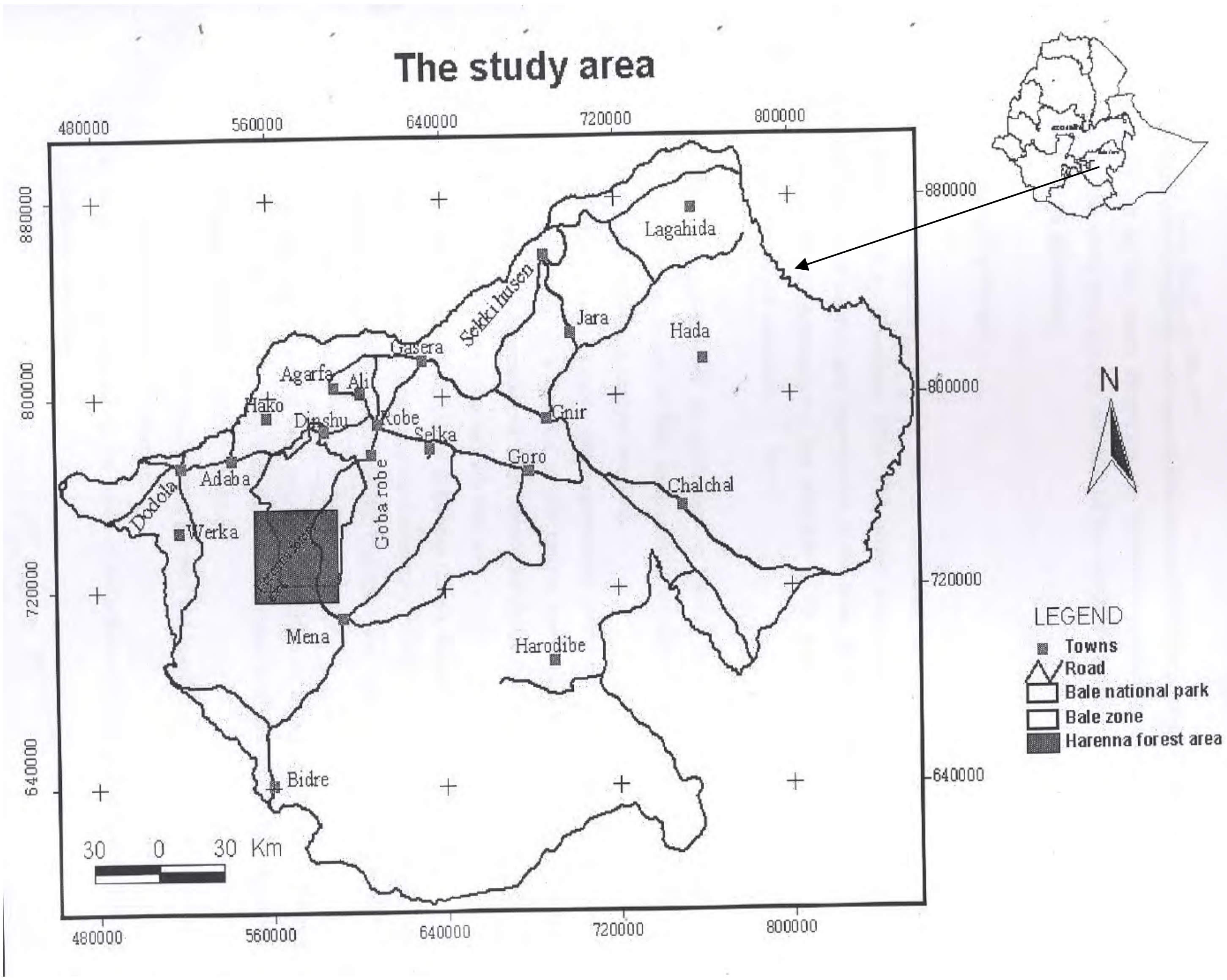

Fig. 1: Location of the study area

4.1.3 Climate and Rainfall

There are no meteorological data specific to the Harena forest although there is a meteorological Station at Dollo Mena. Nevertheless, Harena forest is under the influence of a bi-modal rainfall pattern (Fig. 2). The highest rainfall occurs from March to May and from September to November. Harena forest receives a monthly minimum and maximum temperatures of 15.86 ^{0}C and 28.21 ^{0}C, respectively (NMSA, 2004). Furthermore, the average monthly relative humidity at 1800 m a.s.l is 79.57% and the average monthly wind speed is 10.65 m/sec. The Harena escarpment appears to intercept the flow of moist air events from the south, thus increasing the precipitation in the area where dense mists are formed at higher altitudes for most of the day during the rainy season.

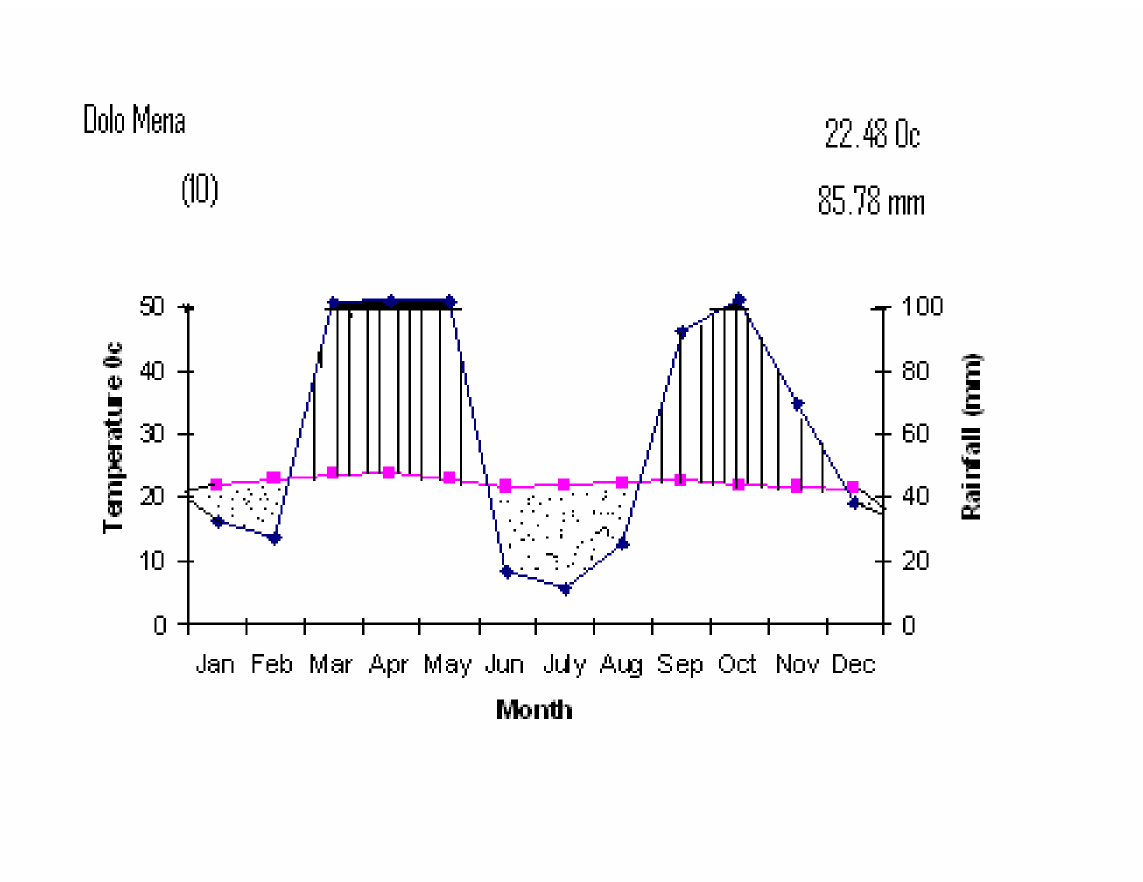

Fig. 2: Mean annual temperature and rainfall at Dollo Mena (1994-2003)

4.1.4 Vegetation

The Harena forest consists of moist afro-montane vegetation. It is composed of vegetation that is structurally and compositionally diverse. According to the ecological study of the forest by Lisanework Negatu and Mesfin Tadesse (1989) the vegetation indicates five vegetation zones.

The lower most portions (1500-1600 m a.s.l) are relatively dry forest and the emergent tree is *Podocarpus falcatus*. At elevation between 1,660 and 1980 m a.s.l the natural vegetation consists of a mixture of *Podocarpus and Pouteria* forest where the upper story is dominated by P*odocarpus falcatus, Pouteria adolfi- friederici* and *Syzygium guineense.*

Altitudes between 1980-2390 m a.s.l are the zones that include the wetter and more humid part of the forest and the upper storey is dominated by *Pouteria adolfi- friederici, Syzygium guineense* and *Prunus africana*. *Schefflera abyssinica* and *Hagenia abyssinica* dominate the vegetation at altitudes from 2390-2800 m.

The higher most portion of the vegetation (2800-3250 m a.s.l) is characterized by *Hypericum revolutum, Erica arborea, Schefflera volkensii* and *Hagenia abyssinica*.

In addition to these, the forest is known for consisting of a variety of endemic plant species as well as those which are economically important. Beside these facts, the Harena forest is a highly disturbed forest due to human encroachment and activities.

4.1.5 Population settlement and land use

Evidences in the past indicate that the permanent settlers of the Harena forest were primarily hunter-gatherers and involved in bee keeping as the main source of their economy. Recently however, following the main road construction from Goba to Dello Mena, some land clearing has already taken place. It is clearly observed that this activity has changed the living conditions of the settlers. Along the main road, encroachment into the forest has been greatly increased and large areas in the forest are getting deforested for agriculture and in these areas, the land is getting over grazed (Fig. 3). In particular, forest areas of the higher altitudes are highly disturbed, making it difficult for one to get undisturbed patches. Even though, it seems bee keeping continues to be the main source of economy of the people, illegal timber production is not uncommon. In fact, there were indications of illegal logging and tree felling that are greatly risking *Hagenia abyssinica* at the time of this study.

Fig. 3: Part of the Harena Forest towards the middle altitude showing a disturbed site

4.2 Vegetation Sampling

A reconnaissance survey of the area under consideration was conducted from December 10-12/2004 to obtain information on the species composition and distribution as well as pattern of canopy gap distribution. The actual fieldwork of data collection on the gap dynamics and regeneration of the forest was undertaken from December 13/2004- January 16/2005 and July 11/2005- August 18/2005.

Gap characteristics and gap makers

What grows up in forest gaps, partly determines the composition of the forest vegetation. Hence, gaps are usually considered as the space in the above ground canopy down to or nearly to ground level which are in some ways, the most important part of the forest growing cycle (Runkle, 1982). So far, researchers have identified two types of gap, i.e., canopy gap, the land surface area directly under the canopy opening, and expanded gap, canopy gap plus the adjacent area extending to the bases of canopy trees surrounding it (Runkle 1981, 1982; Ogden *et al.*, 1991). The later was preferable to the former one as it includes areas directly and indirectly affecting the canopy openings. In the current study, natural gaps were considered as an opening in the upper canopy extending to the bases of canopy trees surrounding the canopy opening (Runkle, 1981).

Gaps were identified at every 25 m altitudinal drop starting from 3000 m a.s.l to 2000 m a.s.l in NW to SE direction following the main road from Goba to Dello Mena. 41 Natural gaps were systematically identified for the current study following this sampling route.

For every gap, the longest distance between any two-canopy trees i.e. gap length and the largest distance perpendicular to the length (i.e. gap width) were measured and the values were fitted in an ellipse formula sensu Runkle (1981), i.e.,

$A = \frac{\pi LW}{4}$ Where A = Gap Area

L = the longest distance

W= the largest perpendicular distance

For all the gaps, the aspect and slope were recorded using compass and clinometer, respectively to find out their influences on the number of seedling and saplings in the sampled gaps.

For each tree that created a gap (gap maker), species name, diameter at breast height (DBH) and type of damage or mode of mortality were determined. Gap formations were classified as (1) standing dead, (2) overthrown (uprooted), (3) snapped bole and (4) branch and/or crown snapped (breakage) (Obiri and Lawes, 2004). In the case of multiple tree falls, the tree that seemed original tree that has caused the gap was considered as the gap maker and was treated as end product of the effect. For branch/crown breakage, DBH of the largest end of the branch was measured following Stewart *et al*. (1991).

Gap ages were estimated from the physical status of the gap makers (state of decay) following Abayneh Derero *et al*. (2003). In judging the age of gaps, assistance of local knowledgeable farmers was sought as well. Gap age was ranked from 1 – 5 following Abayneh Derero *et al*. (2003) where: 1 = 1-3 years; 2= 4-6 years; 3=7-9 years; 4 = 10-12 and 5 = 13 years or more.

In each natural gap, gap filling woody species with a height of less than 2/3 of the canopy tree height were identified to species level. Individuals with a height $\geq$ 1m were considered as saplings and counts were made by species. Individuals with a DBH > 1cm and $\leq$ 10cm were treated as gap fillers. Seedlings were counted in 5 (0.5 m x 0.5 m) plots systematically laid out in each gap to be used to calculate seedling density (Obiri and Lawes, 2004).

To compare species regenerating in gaps with those under canopy, undisturbed sites at least 10 m away from the gaps into the natural forest were systematically selected. An area equivalent to that of the respective gap was measured. Saplings (height ≥ 1m) were counted by species. Seedlings of woody species were counted in 5 (0.5m x 0.5m) plots systematically laid out for seedling density calculation.

To study the relationships between the forest canopy species and the soil seed bank, soil samples were systematically collected from all gaps subjected to the current study. Soil samples were taken from an area of 15 cm x l5 cm at the depths of 0-3 cm, 3-6 cm and 6-9 cm separately (Demel Teketay and Gransterom, 1995) by using a knife along the longer dimension of the gap, from the center and four corners of the gaps. Then, the soil samples from five points of the same depth were thoroughly mixed to get a composite mixture and 1/5 of this mixture was put in a cotton bag, tied and properly labeled. Samples were collected in this manner from all depths of all gaps and undisturbed canopy sites. All the soil samples were brought to the Green House of the Department of Biology, Addis Ababa University for germination trial. Germination was made in plastic germination trays and the samples were being watered once every day and depending on the need. The germinating seedlings were recorded every two weeks for six months. The seedlings were allowed to grow further until identification is possible.

Identification of specimens to family and species level was done at the National Herbarium of Addis Ababa University. During identification, taxonomic keys and herbarium collections were used. Furthermore, Flora of Ethiopia and Flora Ethiopia and Eritrea were also used. In the case of the identification of soil seed bank germinant, specialists were also consulted. Plant Nomenclature follows published volumes and unpublished manuscripts of Flora of Ethiopia and Eritrea.

4.3 Data Treatment and analysis

In order to see if there is any relationship between altitude, gap size, slope, species richness, number of saplings and gap fillers, correlation analysis was done by taking two of them at a time. The effect of gap size on the number of species and number of sapling was tested by linear regression analysis by using SPSS window for version 10. Gap size partitioning among the gap filler species was checked by examining the frequency distribution of species, their maximum occurrence (highest abundance versus gap size) and identification of those species that were confined to either small or large gaps following Obiri and Lawes (2004).

Species replacement probabilities of gaps were estimated for the gap maker species by using the relative abundance of recruits ≥ l cm and≤ l0 cm DBH of a species in gaps created by the same or another species. This was achieved by counting the number of gap fillers of a given species and expressing it as a proportion of the total number of gap fillers per gap maker following Runkle (1981) and Obiri and Lawes (2004).

The differences in soil seed banks of the soils collected from canopy opening and closed canopy and their corresponding three layers of soil were described by using descriptive statistics.

5 RESULTS

5.1 Mode of Mortality and Gap Characteristics

Natural gaps in the Harena forest were caused by four mechanisms. Gaps caused by overthrow have been encountered most commonly (51.2%, n=21) in the 41 gaps subjected to the current study. These were followed by the gaps caused by branch/crown breakage (34.2%, =n-14). Gaps caused by dead but standing (snags in the terminology of Obiri and Lawes, 2004) and bole snapping were identified as having the lowest values (7.3%, n=3 for each). Of the 41 natural gaps, 56.6%, n = 23 were caused by multiple tree falls and the rest 43.4%, n=18 were due to single tree fall.

The total area of the expanded gap was 1.2 hectare, with mean gap size of 289.74±165.48 m^2 (mean ± sd, n=41). The median gap area was found to be 266.90m^2 that is almost close to the mean. Gap size ranged from 101.03 - 896.93 m^2. The difference in gap area among types of the gap was found to be significant ($F_{3, 37}$=4.98, $p< 0.01$, Table 1).

Gaps created through overthrow were the largest in area and is followed by those caused by bole snapping. Gaps created through branch/crown breakage and dead standing were relatively small in area (Table 1).

Most of the gaps had an area that falls between 150 m^2 – 349 m^2, i.e., 63.4% of the gaps. While 3 gaps were grouped as having the highest gap size class, i.e., > 650 m^2, a total of 6 gaps were found to have the smallest gap size class, i.e. < 150m^2. On the other hand, gap size classes 4 and 5 which have an Area of 350 – 449 m^2 and 450-549 m^2, respectively, were the least encountered ones during this study (Figure 4).

Gap ages have ranged from 1-15 years (Appendix 1). Natural gaps that have aged 4-6 years were most commonly encountered (26.3%). Those aged 7-9 years were the second (22%, n=9) most common ones whereas gaps of ages 1-3 years have constituted about 17.1% of the gaps. Finally, the oldest identified gaps (>13 years) have accounted only for 7.3% (Fig. 5).

The slopes of the gaps studied ranged between 0-30%, with an average slope of 13.12%. Of the 41 gaps, 46.34% (n = 19) were oriented in a SE direction, 31.7% (n = 13) to SW, 9.76% to NE and 7.32% were directed to NW directions respectively. Two of the remaining gaps have an East or West direction (Fig. 6).

5.2 Features of Gap Maker Species and Their Distribution

A total of fourteen different species of canopy trees were involved in gap formation. Out of these, *Dombeya torrida* was the most common gap maker (17.07%; n=7) and *Hagenia abyssinica* was the second most one (12.19%, n=5). The least common gap makers were examplified by *Bersama abyssinica, Diospyros abyssinica* and *Schefflera abyssinica* where each of them has contributed about 2.44% of the fourteen species (Table 2).

Gap maker species have exhibited variations in their sizes. The mean DBH of the gap makers was 50.4 cm (n=41). Those gaps makers of the bole snapped category had the highest mean DBH i.e. 55.41 cm while those in the overthrown had a DBH of 53.19 cm, n=22). On the other hand, a DBH of trees that died standing (snags) and broken branches/crown were found to be relatively small, i.e. 48.94 cm and 46.47 cm respectively.

Schefflera abyssinica was the main gap maker species in terms of mean DBH (92.36 cm). Nevertheless, the contributions of *Prunus africana, Erythrina brucei* and *Schefflera volkensii* with the mean DBH, 85.99 cm, 82.81 cm and 82.41 cm respectively are also remarkable. On the other hand, *Syzygium guineense, Bersama abyssinica* and *Diospyors abyssinica* were found to have the smallest DBH values. Furthermore, the mean DBH values of the remaining gap makers falls in the range of the highest and lowest last values (Table 2).

Table 1: Gap characteristics of all sampled natural gaps in Harena Afromontane forest.

Dimensions	Bole snapped	Branch/crown Breakage	Overthrown	Standing dead (snags)	Total
Number of gaps	3	14	21	3	41
Mean ± 1 sd (gap area m^2)	294.64 ±277.65	270.26 ±129.32	319.35 ±195.10	168.51 ±59.57	289.74 ±165.48
Median gap area (m^2)	314	252.77	313.22	188.40	266.90
Range in gap area (m^2)	141.30-428.61	150.72-685.71	101.03-896.93	103.62-213.52	101.03-896.93
Percentage of gaps	7.32	34.15	51.22	7.32	100

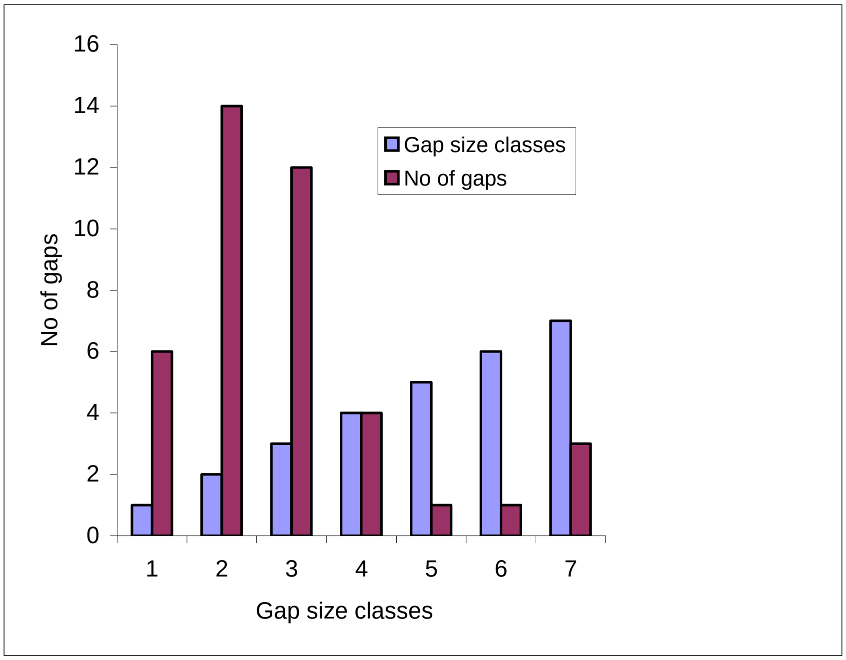

Fig. 4: Distribution of gaps into gap size classes= <150 m^2, 2=150-249 m^2, 3=250-349 m^2 4=350-449 m^2 5=450-549 m^2 6= 550-649 m^2 7= >650 m^2

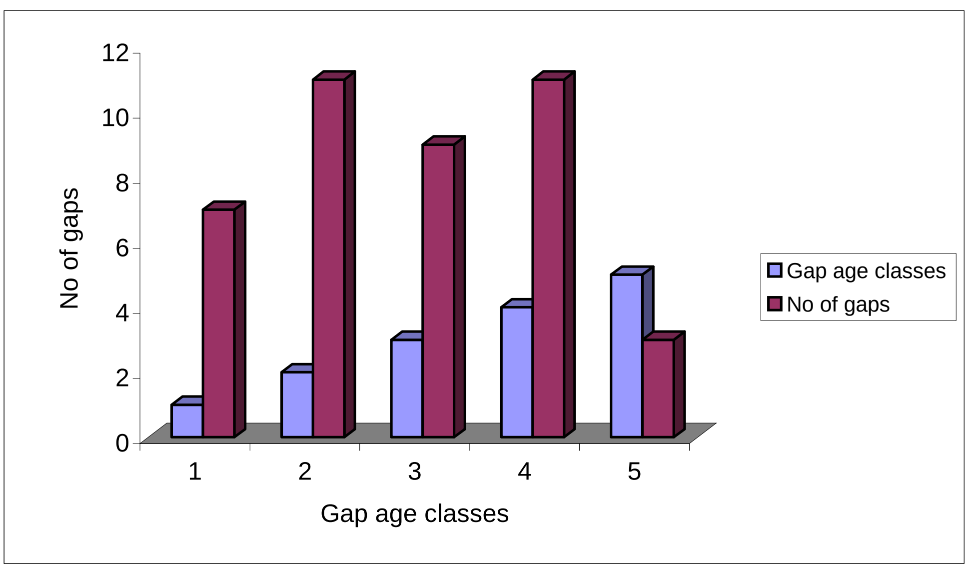

Fig. 5: Distribution of gaps into gap age classes: 1 = 1-3 yrs, 2 = 4-6 yrs, 3 = 7-9 yrs, 4= 10- 12 yrs, 5= ≥13 yrs

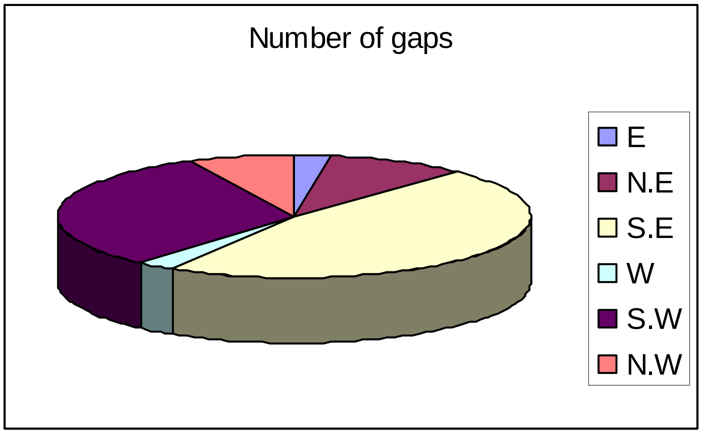

Fig. 6: Number of gaps in different orientations

The fourteen gap maker species were not equally encountered at different altitudes. At the higher altitudes (2850-3000m a.s.l), *Hagenia abyssinica*, *Myrsine melanophloeos* and *Hypericum revolutum* were the most common gap maker species, even though *H. abyssinica* occurs down to 2225 m a.s.l. *Schefflera volkensii* and *Galiniera saxifraga* were dominating gap maker species between 2675-2825 m a.s.l while *Dombeya torrida* was the only gap maker species that was encountered from 2500-2650 m a.s.l. On the other hand, *Prunus africana*, *Croton macrostachyus* and *Syzygium guineense* were the gap maker species important at attitudes 2300-2000 m a.s.l (Table 3).

Table 2 Types of gaps, gap maker species and their DBH and percentage in Harena Afromontane forest

		Mode of mortality					
Gap makers	No. Of gap makers	Over thrown	Bole Snapped	Dead Standing	Branch Breakage	Mean DBH (cm)	% of gap makers
Dombeya torrida	7	3	1	0	3	51.19	17.07
Hagenia abyssinica	5	2	0	2	1	54.65	12.19
Croton macrostachyus	4	3	0	0	1	54.78	9.76
Allophylus abyssinicus	4	4	0	0	0	39.59	9.76
Galiniera saxifraga	3	1	0	0	2	54.14	7.32
Hypericum revolutum	3	1	0	1	1	20.7	7.32
Myrsine melanophloeos	3	1	1	0	1	28.56	7.32
Schefflera volkensii	3	2	1	0	0	82.41	7.32
Erythrina brucei	2	1	0	0	1	82.81	4.88
Prunus africana	2	2	0	0	0	85.98	4.88
Syzygium guineense	2	0	0	0	2	26.55	4.88
Bersama abyssinica	1	1	0	0	0	19.11	2.44
Diospyros abyssinica	1	0	0	0	1	19.88	2.44
Scheflera abyssinica	1	0	0	0	1	92.36	2.44
Total(n)	41	21	3	3	14		
Mean DBH(cm)	50.4	53.19	55.41	48.94	46.74		

Table 3: Altitudinal occurrence of gap maker species

Gap Maker Species	**Altitude (m asl)**
Hagenia abyssinica	3000-2225
Myrsine melanophloeos	2950-2775
Hypericum revolutum	2925-2875
Galiniera saxifraga	2825-2425
Schefflera volkensii	2800-2675
Dombeya torrida	2650-2500
Diospyros abyssinica	2475
Schefflera abyssinica	2450
Allophylus abyssinicus	2400-2075
Prunus africana	2300-2025
Erythrina brucei	2275-2250
Bersama abyssinica	2200
Croton macrostachus	2175-2050
Syzygium guineense	2100-2000

5.3 Gap Regeneration of Woody Species

5.3.1 Composition and densities of regenerating seedlings of the gaps

Seedlings of 14 different woody species were encountered during the current study (Table 4). The aggregate density of these seedlings was 48,720 individuals/hectare. *Myrsine melanophloeos* was found to have the highest seedling density (13268 individuals/hectare) while *Brucea antidysenterica* had the second highest seedling density (11707 individuals/hectare) in the natural gaps studied. On the other hand, the smallest seedling density (195 individuals/ hectare) was recorded in *Cassipourea malosana* (Table 4). Note that both *Allophylus abyssinicus* and *Ficus sur* have the same seedling density (390 individuals/ hectare).

5.3.2 Composition and density of saplings

A total of 24 woody species were recorded inside the sampled natural gaps (Table 4). The aggregate density of saplings was 678 individuals/hectare. *Brucea antidysenterica* had the most common sapling (31.42%, n=213). Sapling of *Lepidotrichilia volkensii, Vepris dainellii* and *Bersama abyssinica* have accounted for 18.44%, 11.50% and 9.88%, respectively. On the other hand, the smallest proportion of saplings, *i.e.,* less than 1%, characterizes *Pouteria adolfi-friederici, Syzygium guineense, Pittosporum viridiflorum, Dombeya torrida, Discopodium eremanthum and Erythrina brucei*. The density of saplings of *Myrsine melanophloeos* has accounted for 7.08% while that of *Diospyros abyssinica* is 5.75%. Furthermore, saplings of *Prunus africana*, *Cassipourea malosana, Croton macrostachyus*, *Canthium oligocarpum* and *Galiniera saxifraga* accounted for less than 5% (Table 4).

5.4 Regeneration of Woody Species Under Closed Forest Canopy

5.4.1 Composition and density of seedlings

Eleven woody species were found regenerating under a closed forest canopy (Table 4). The aggregate density of the seedlings was found to be 31,417 individuals/hectare. Out of these, seedlings of *Brucea antidysenterica* were the most abundant (27.98%, n = 8780 individuals/hectare) followed by those of *Vepris dainellii.* The least density of seedlings of *Geliniera saxifraga* (195 individuals/ hectare) was encountered under forest canopy in the current study. Although the magnitude of the density of their seedlings falls in the extreme ranges defined above, seedlings of *Bersama abyssinica* and *Lepidotrichilia volkensii* were also recorded under canopy.

*5.4.*2 Composition and density of saplings

Saplings of 18 woody species with an aggregate density of 498 individuals /hectare were recorded under closed forest canopy. *Lepidotrichilia volkensii* had the most abundant saplings (29.12%, n=120) while the least values were recorded for *Pittosporum viridiflorum, Erythrina* *brucei, Prunus africana* and *Vernonia amygdalina* (0.20%, n=1, each). Saplings of *Brucea antidysenterica, Vepris dainellii*, *Diospyros abyssinica*, *Bersam*a *abyssinica* and *Dracaena afromontana* have constituted 25.3%, 15, 7%, 6.6%,4 .8% and 3.2% of the total sapling density, respectively. The sapling densities of *Myrsine melanophloeos, Maytenus undata* and *Allophylus abyssinicus* have contributed 3%, 2.8% and 2.6% respectively. The remaining species such as *Canthium oligocarpum*, *Cassipourea malosana Discopdium eremanthum, Galiniera saxifraga* and *Pouteria adolfi-friederici* have accounted only 1-2% of the total density (Table 4).

Table 4. Seedlings and saplings of woody species and their density under forest canopy in Harena Afromontane forest

Gap filler species	**No in gaps**		**No under closed canopy**	
	Seedlings	**Saplings**	**Seedlings**	**Saplings**
Allophylus abyssinicus	390	6	0	13
Bersama abyssinica	7415	67	4098	24
Brucea antidysenterica	11707	213	8780	126
Buddleja polystrachya	0	3	0	0
Canthium oligocarpum	585	8	0	8
Cassipourea malosana	195	11	390	8
Croton macrostachyus	3122	10	0	0
Diospyros abyssinica	1951	39	1561	33
Discopodium eremanthum	585	4	390	5
Dombeya torrida	0	1	0	0
Dracaena afromontana	0	4	0	16
Erythrina brucei	0	1	0	1
Ficus sur	390	2	0	0
Galiniera saxifraga	0	8	195	4
Hypericum revolutum	0	0	390	0
Lepidotrichilia volkensii	6049	125	4683	145
Maytenus undata	1171	22	1369	14
Pittosporum viridiflorum	0	1	0	1
Pouteria adolfi-friederici	0	3	0	4
Polyscias fulva	0	5	0	0
Prunus africana	585	14	0	1
Myrsine melanophloeos	13268	48	4488	15
Syzygium guineense	0	3	0	0
Vepris dainellii	3307	78	5073	79
Vernonia amygdalina	0	2	0	1
Total	48720/hectare	678/hectare	31417/hectare	498/hectare

5.5 Regeneration and Recruitments in Forest Gaps and Under Closed Forest Canopy

A seedling density of gaps and closed forest canopies has revealed variations concerning the regeneration and recruitments of woody species (Fig. 7). For example, seedlings of ***Galiniera saxifraga*** and ***Hypericum revolutun*** were not encountered in gaps but found under closed forest canopy. On the other hand, seedlings of ***Allophylus abyssinicus***, ***Cassipourea malosana***, ***Croton macrostachyus***, ***Ficus sur*** and ***Prunus africana*** were common in the forest gaps but missing from under closed forest canopy. Concerning the density of seedlings, ***Myrsine malanophloes, Bersama abyssinica***, ***Discopodium eremanthum***, ***Brucea antydysenterica Lepidotrichilia volkensii*** and ***Diospyros abyssinica*** were found to have more seedlings in forest gaps than forest canopy while ***Vepris dainellii***, ***Cassipourea malosana*** and ***Maytenus undata*** have exhibited decreasing values in their seedling density (Fig. 7).

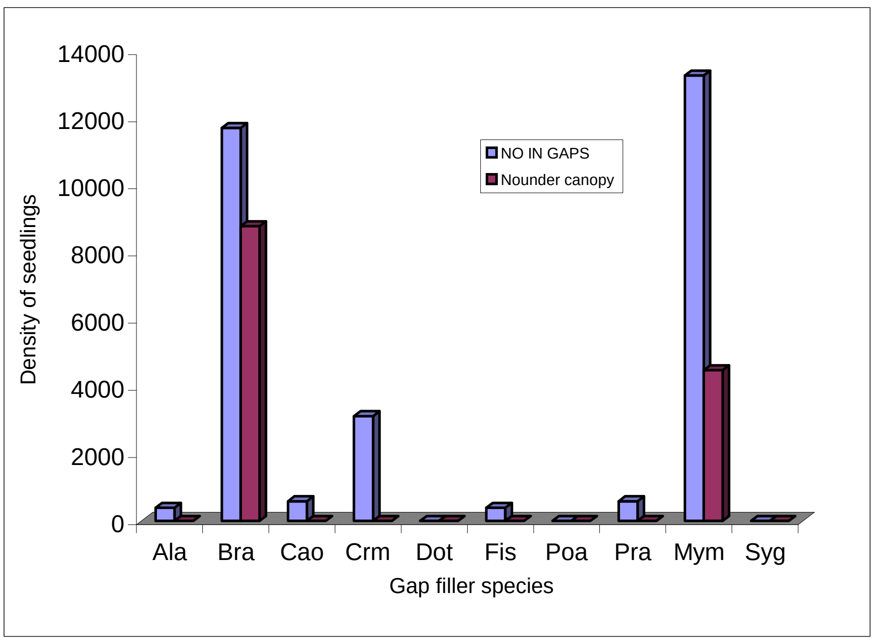

Fig. 7: A comparative density of seedlings in the forest gaps and closed forest canopies in Harena Afromontane forest.

Abbreviations:Ala=*Allophylus abyssinicus;* Bra=*Brucea antidysenterica;* Cao = *Canthium oligocarpum*; Crm = *Croton macrostachyus*; Dot=*Dombeya torrida*, Fis=*Ficus sur*; Poa=*Pouteria adolfi –friederici*, Pra=*Prunus africana;* Mym=*Myrsine melanophloeos;* Syg=*Syzygium guineense*

As is the case with seedlings, saplings of gap-fillers has exhibited remarkable variations both in forest gaps and forest canopy in relation to density and occurrence (Fig. 8). Saplings of six species were recorded growing in forest gaps but missing from under forest canopies. These missing species are *Buddleja polystachya*, *Croton macrostachyus*, *Dombeya torrida*, *Ficus sur*, *Polyscias fulva* and *Syzygium guineense*. As a rule, the regeneration and recruitment status of species varies both in the forest gaps and under forest canopy. For example, *Prunus africana* has shown an increment of 1300% in the number of saplings in forest gaps when compared to the saplings under closed forest canopy. Similarly, more saplings were recorded in forest gaps than under closed forest canopy for *Myrsine melanophloeos*, *Bersama abyssinica*, *Galiniera saxifraga* and *Vernonia amygdalina*, *Brucea antidysenterica*, *Maytenus undata*, *Cassipourea malosana* and *Diospyros abyssinica.* On the other hand, *Allophylus abyssinicus*, *Poutria adolfi-friederici*, *Discopodium eremanthum*, *Lepidotrichilia volkensii* and *Vepris dainellii* had less number of saplings in forest gaps than under closed forest canopy (Fig. 8). Contrary to the aforementioned conditions, *Canthium oligocarpum*, *Erythrina brucei* and *Pittosporum viridiflorum* have shown the same density of saplings both in forest gaps and closed forest canopy.

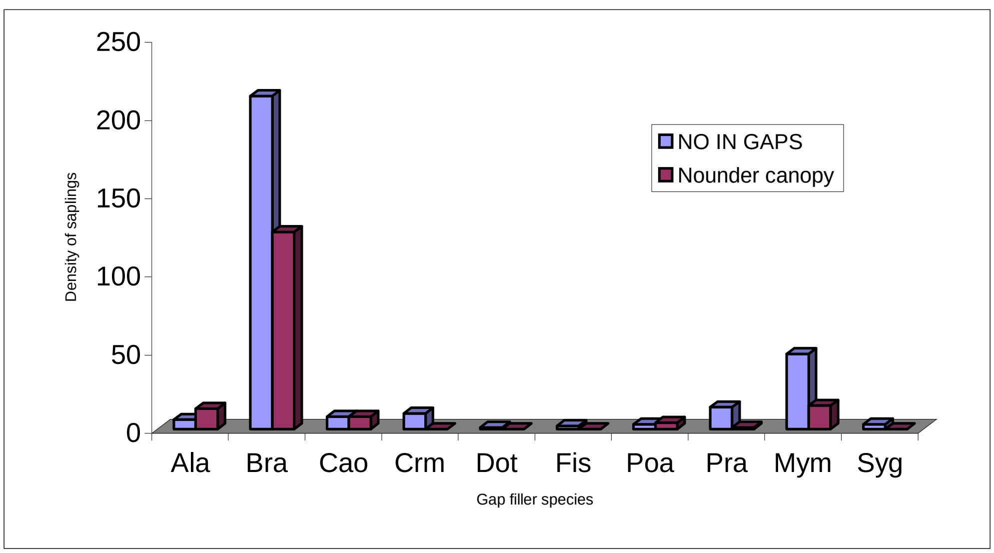

Fig. 8. A comparative density of saplings in forest gaps and under closed forest canopies of Harena Afromontane forest (Abbreviations as of Fig.7)

5.6 Survivorships of Gap-fillers

Gap-filler species have shown differential survivorship in the current study (Fig. 9). For example, ***Bersama abyssinica***, ***Diospyros abyssinica*** and ***Brucea antidysenterica*** have comparable survivorship curves. Whereas, ***P. adolfi-friederici*** had a minimum survivorship of its small-sized saplings (1 – 2.5 m), and Syzygium ***guineense*** had a minimum survivorship of its middle sized saplings (1.5-2.5m). Furthermore, ***Prunus africana*** saplings showed zigzag pattern of survivorship.

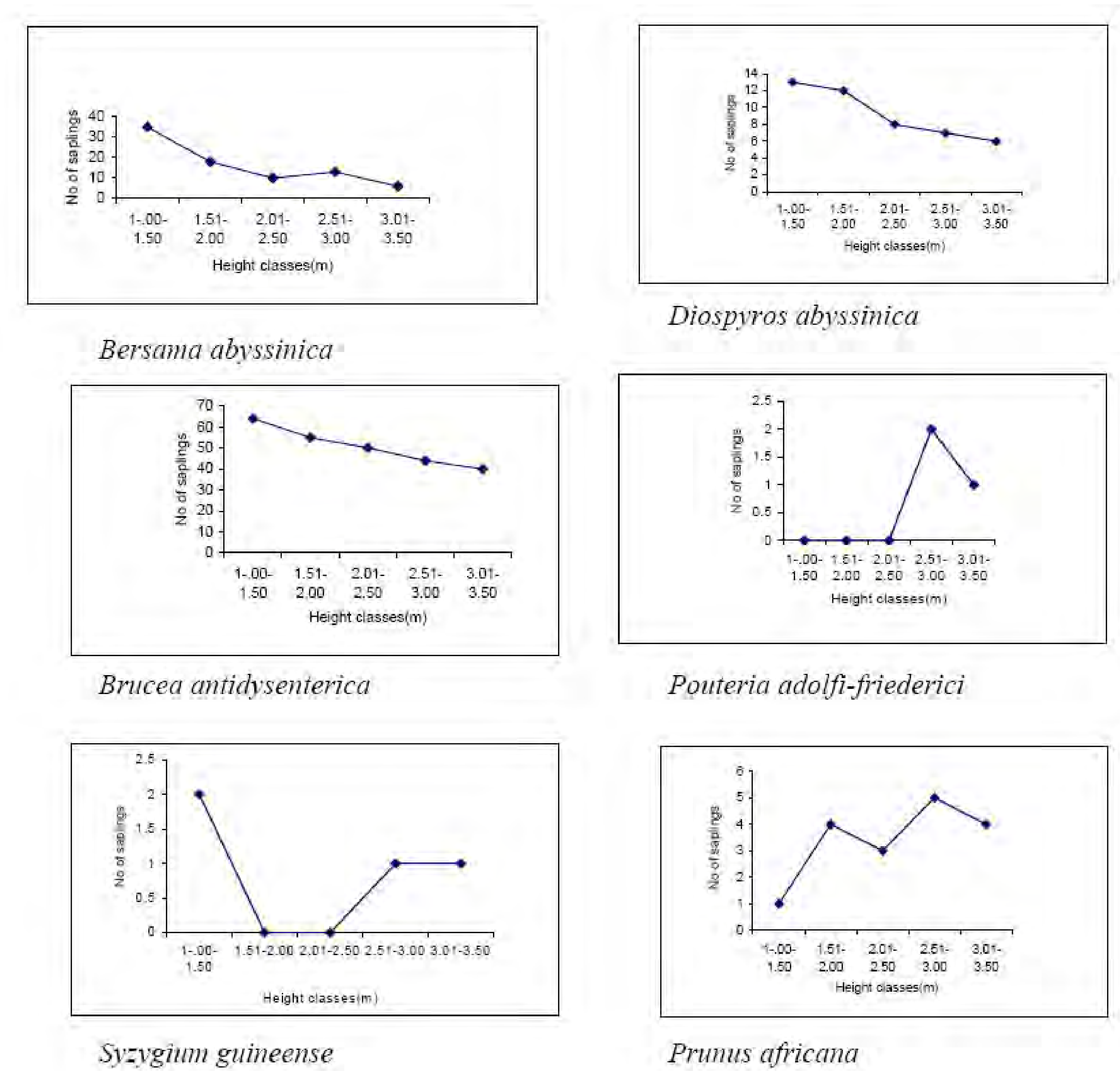

Fig. 9. Survivorship curves of selected gap-filler species in the Harena Afromontane forest.

5.7 Gap Regeneration and Altitude

A strong negative correlation was found between altitude and the number of regenerating woody species in forest gaps ($r = -0.730$, $p \leq 0.01$). The number of saplings and gap fillers was also negatively correlated to altitude (Table 5).

Table 5: Pearson's correlation of altitude, slope and species, number of saplings and gap fillers by taking two at a time

	Altitude (m)	Slope (%)	No woody Species	No of Saplings
Altitude	-			
Slope	-			
No W. species	-0.730**	-0.476**		
No of saplings	-0.677**	-0.579**	0.543**	
No gap fillers	-0.629**	-0.560**	0.405**	0.909**

** = p< 0.01

At an altitudinal range of 3000-2800 m a.s.l, only eight woody species were found to regenerate in the forest gaps. The seedling density and sapling density of these species were 7609 individuals/hectare and 61 individuals/hectare, respectively. The highest seedling density was recorded for *Myrsine melanophloeos* (6244 individuals/hectare) while the highest sapling density characterizes *Brucea antidysenterica* (34individuals/hectare) – Table 6. Furthermore, *Discopodium eremanthum, Bersama abyssinica, Brucea antidysenterica* and *Maytenus undata* have shown a seedling density of 585,390 and 195 individuals/hectare, respectively. Note that the density of sapling for *Myrsine melanophloeos* was found to be 15 individuals/hectare,while *Bersama abyssinica*,*Pittosporum viridiflorum* and *Vernonia amygdalina* were each represented by the smallest sapling density (Table 6).

The smallest number of gap filling species has characterized an altitudinal range of 2800-2600 m a.s.l where only seven species were recorded. The densities of seedling and sapling for this range were 9560 and 130 individuals/hectare, respectively. *Myrsine melanophloeos* had the highest seedling density (n=7024; 73.5%) while *Brucea antidysenterica* was found to have the highest sapling densities (n=78; 60%). The latter had a seedling density of 22.5%, i.e., 2146 individuals/hectare whereas saplings of *Myrsine melanophloeos* have constituted 30%. On the other hand, the seedling density of *Maytenus undata* was found to be 390 individuals/ hectare.*Allophylus abyssinica*,*Bersama abyssinica*,*Buddleja polystachya* and Lepidotrichilia *volkensii* had no seedlings at this altitudinal range (Table 6).

The third altitude range (2600 - 2400 m asl) has consisted of 11 gap- regenerating woody species. The total seedling density was 5659 individuals/hectare while the sapling density was 134 individuals/hectare in this range. It was found that *Bersama abyssinica* has the highest seedling and sapling densities (Table 6) and followed by *Brucea antidysenterica* concerning the seedling density (n=1366,24.1%) and *Lepidotrichilia volkensii* with regard to sapling density (23.88%, n=32). However, the seedling density of *Lepidotrichilia volkensii* was about 20.7% of the total seedling density whereas *Brucea antidysenterica* has accounted for 22.39% of the total sapling density. On the other hand, *Dombeya torrida* and *Vernonia amygdalina* have exhibited the least sapling density (0.75% each). Noteworthy is that *Buddleja polystacyea, Cassipourea malosana, Dombeya torrida, Galiniera saxifraga, Maytenus undata, Myrsine melanophloeos* and *Vernonia amygdalina* have lacked seedling (Table 6).

Thirteen species were recorded from the forest gaps located at altitude range of 2400 - 2200 m a.s.l. The total seedling and sapling densities of this range were 9170 and 208 individuals/hectare, respectively. *Brucea antidysenterica* and *Lepidotrichilia volkensii* have constituted 29.8% of the total seedling density each. Concerning sapling density *Lepidotrichilia volkensii* (44.71 %) and *Brucea antidysenterica* (15.87%) were the first and second most important forest gap regenerating species at this range. *Allophylus abyssinicus*, *Erythrina brucei* and *Prunus africana* have exhibited the smallest sapling density (0.48%, n=1, each). Regarding seedling density, no seedling of *Diospyros abyssinica, Erythrina brucei*, *Galiniera saxifraga*, *Maytenus undata*, *Polyscias fulva* and *Prunus africana* was encountered at this altitude range.

Both *Canthium oligocarpum* and *Cassipourea malosana* were represented by equal number of seedlings (195 individuals/hectare each), while *Vepris dainellii* was represented by a seedling density of 780 individuals /hectare (Table 6).

It is to be noted that maximum numbers of forest gap regenerating woody species were encountered in the last altitudinal range (2200-2000 m a.s.l). Sixteen species were recorded here. Examples are *Allophylus abyssinicus,Canthium oligocarpum*, *Croton macrostachyus*, *Dracaena afromontana Diospyros abyssinica,Galiniera saxifraga*, *Ficus sur*, *Poutera adolfi-friederici*, *Syzygium guineense* and *Vepris dainellii* were some of the forest gap regenerating in this altitudinal range (Table 6). The seedling and sapling densities of this range were the highest of any of the altitudinal ranges (seedling density = 18730 individuals/hectare and sapling density = 272individuals/hectare) presented above. *Brucea antidysenterica* had the highest seedling and sapling densities (28.1% for seedlings and 28.8% for saplings). On the other hand, *Bersama abyssinica* and *Vepris dainellii* have each accounted for 13.6% of the total seedling density but only *Vepris dainellii* has contributed 25.83% to the total sapling density. The density of *Maytenus undata* has shown an increase as compared to other altitudinal ranges, even though *Lepidotrichilia volkensii* had exhibited a relative decrease in density as compared to that of 2400-2200 m a.s.l. Furthermore, a seedling density of 585 and a sapling density of 16 individuals / hectare characterize *Prunus africana* at this altitudinal range.

Table 6: Densities of seedlings and saplings of gap filling woody species at different altitudinal ranges/hectare

Attitudinal range	Species	Seedling density/ha	Sapling density/ha
3000-28000 masl	***Bersama abyssinica***	390	1
	Brucea antidysenterica	195	34
	Discopodium eremanthum	585	5
	Galiniera saxifraga	0	2
	Maytenus undata	195	2
	Pittosporum viridiflorum	0	1
	Myrsine melanophloeos	6244	15
	Vernonia amygdalina	0	1
		7609	61
2800-2600masl	***Allophylus abyssinicus***	0	1
	Bersama Abyssiica	0	7
	Brucea antidysenterica	2146	78
	Buddleja polystachya	0	1
	Lepidotrichilia volkensii	0	1
	Maytenus undata	390	3
	Myrsine melanophloeos	7024	39
		9560	130
2600-2400 masl	***Bersama abyssinica***	2146	34
	Brucea antidysenterica	1366	30
	Buddeleja polystachya	0	2
	Cassipourea malosana	0	4
	Diospyros abyssinica	976	24
	Dombeya torrida	0	1
	Galiniera saxifraga	0	2
	Lepidotrichilia volkensii	1171	32
	Mayteus undata	0	2
	Myrsine melanophloeos	0	2
	Vernonia amygdalina	0	1
		5659	134
2400-2200 masl	***Allophylus abyssinicus***	195	1
	Bersama abyssinica	2341	21
	Brucea antidysenterica	2732	33

	Canthium oligocarpum	195	5
	Cassipourea malosana	195	8
	Diospyros abyssinica	0	9
	Erythrina brucei	0	1
	Galienera saxifraga	0	3
	Lepidotrichilia volkensii	2732	93
	Maytenus undata	0	4
	Polyscias fulva	0	6
	Vepris dainellii	780	23
	Prunus africana	0	1
		9170	208
2200-2000 masl	***Allophylus abyssinicus***	195	6
	Bersama abyssinica	2537	17
	Brucea antidysenterica	5268	78
	Canthium oligocarpum	390	4
	Cassipourea malosana	0	1
	Croton macrostachyus	3121	12
	Diospyros abyssinica	976	13
	Dracaena afromontana	0	5
	Ficus sur	390	2
	Galiniera saxiffaga	0	3
	Maytenus undata	3585	15
	Lepidotrichlia volkensii	2146	23
	Pouteria adolfi- friederici	0	3
	Prunus africana	585	16
	Syzygium guineense	0	4
	Vepris dainellii	2537	70
		18730	272

5.8 Gap Age and Regeneration

The following forest gap age classes were suggested in this study, i.e., classes 1 (1-3 years), 2 (4-6 years), 3 (7 -9 years), 4 (10-12 years) and 5 (13 or more years). A comparative analysis of seedling density of all gap age classes has revealed that the maximum seedling density (17562 individuals/hectare) was in gap age class 2 while the youngest gap age class 1 has displayed a seedling density of 12293 individuals/hectare (Fig. 10.1). Furthermore, seedling densities of 10338, 4683 and 3844 individuals/hectare were recorded for gap age classes 4, 5 and 3, respectively. With regard to sapling density, the highest value was recorded for gap age class 1 (931 individuals/hectare) and the lowest for the gap age class 3 (423 individuals/ hectare).

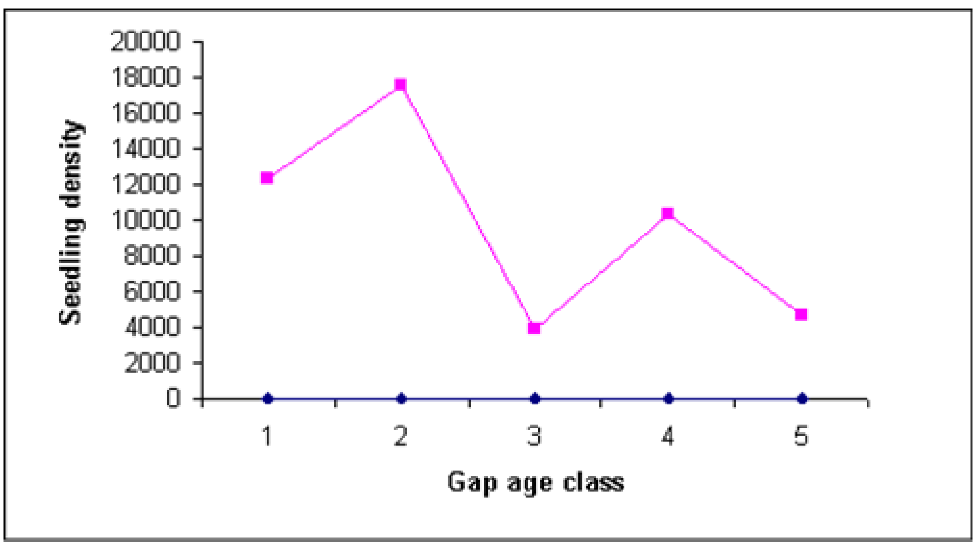

Fig. 10.1 Seedling density/hectare in different gap age classes

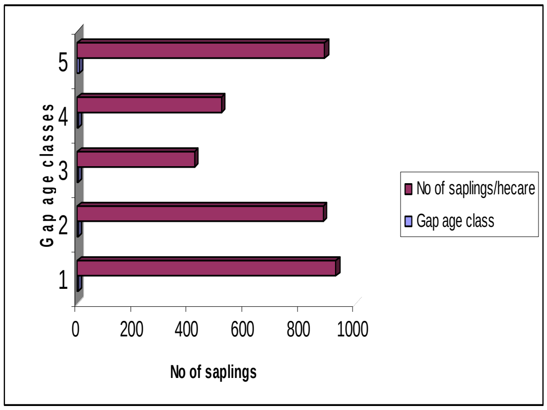

Fig. 10.2: Sapling density/hectare in different gap age classes

5.9 Slope versus Gap Regeneration

The slope of the gaps was found to play important roles in the forest gap regeneration of the Harena forest. Slope was negatively correlated to the number of gap filling woody species (r = -0.476, p≤ 0.01). The number of saplings and gap-fillers was also negatively correlated to slope (r = 0.579 and -0.560, p≤ 0.01, respectively). Species richness and sapling density were usually high at less sloppy gaps. Whereas the maximum seedling density has characterized forest gaps oriented to East direction (39989 individuals/ hectare), only 8731 individuals/hectare were recorded for those facing West direction. The same pattern was also recorded for saplings, i.e., higher for East-facing forest gaps (557 individuals /hectare) than West facing ones (121 individuals /hectare).

5.10 Gap Size Partitioning

In the current study, gap size partitioning was not recognized. A linear regression analysis has shown that gap size does not affect the number of forest gap regenerating woody species (r^2 = 0.027, F=2.127, p ≤ 0.153, Table 7). Furthermore, gap size has also no significant influence on sapling density (r^2= -0.014, F=0.56, p ≤ 0.503, Table 8). Most of the gap filling species occurred at the available forest gaps regardless of size as determined by species altitudinal ranges (Table 9). Furthermore, different species have exhibited variable values of regeneration in different forest gap sizes. For example, whereas *Diospyros abyssinica*, *Maytenus undata* and *Vepris dainellii* have shown maximum regeneration status at the forest gap size of 153.08 m^2, *Allophylus abyssinicus*, *Brucea antidysenterica* and *Galiniera saxifraga* in 282.60 m^2 (Table 9).

Table 7: Model Summary of regression analysis of gap size over number of gap-filler species

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.227[a]	.052	.027	2.4255

a. Predictors: (Constant), GAP SIZE.

ANOVA [b]

Model	Sum of Squares	df.	Mean Square	F	Sig.
1 Regression	12.515	1	12.515	2.127	.153[a]
Residual	229.436	39	5.883		
Total	241.951	40			

a. Predictors: (Constant), GAP SIZE

b. Predictors: (Constant), GAP SIZE.

Table 8: Model Summary of regression analysis of gap size over number of saplings of gap filler species

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.108[a]	.012	-0.014	14.0993

a. Predictors :(constant), Gap Size

ANOVA [b]

Model	Sum of Squares	df.	Mean Square	F	Sig.
1 Regression	90.657	1	90.657	.56	.503
Residual	7752.855	39	198.791		
Total	7843.512	40			

a. Predictors:(constant), Gap Size

b. Dependent variable: Sapling density

Table 9: Gap sizes over which gap filler species encountered and where they are found in maximum abundance

Gap filler species	Gap sizes (m^2)	Gap size harboring maximum abundance
Myrsine Melanophloeos	141.30, 213.52, 238.64, 266.90, 276.32, 282.60, 314,370.91,428.61, 483.56, 896.93	276.32
Brucea antidysenterica	103.62, 141.30, 142,87, 153.08, 163.28, 175.84, 188.4, 196.97, 219.80, 238.64, 266.90, 268.47, 276.32, 280.15, 282.60, 313.22, 314, 333.86, 360.32, 370.91, 428.61, 483.56, 551.07, 653.12, 685.71, 896.93	282.60
Maytenus undata	153.08, 163.28, 188.40, 197.82, 200.96, 268.47, 282.60, 314	153.08
Galiniera saxifraga	188.40, 197.82, 219.80, 268.47, 282.60, 314, 483.56	282.60
Bersama abyssinica	103.62, 142.87, 188, 197, 200, 219, 238, 266.90, 268.47, 282,6, 313.22, 314, 360.32, 373.66, 483.56, 551.07, 653.12	373.66
Vernonia amygdalina	188.40, 266.90, 314	314
Allophylus abyssinicus	103.62, 282.60, 360.32	282
Erythrina brucei	200.90	200.90
Croton macrostachyus	101.03, 142.87, 175.84, 196.97, 282.60	175.84
Dracaena afromontana	142, 197.82, 314.31	314.31
Polyscias fulva	268.47	268
Pouteria adolfi- friederici	197.97	197.97
Syzygium guineense	196.97, 200.96	196
Prunus africana	101.03, 314.14	314.14
Vepris dainellii	101.03, 103.62, 142.87, 153.08, 175.84, 188.40, 196.97, 197.82, 200.96, 268.47, 280.15, 314.31	153.08
Ficus sur	101.03	101.03
Lepidotrichilia volkensii	103.62, 142.87, 150.72, 153.08, 175.84, 188.40, 196.97, 197.82, 200.96, 266.90, 268.47, 276.32, 280.15, 282.60, 268.47, 313.22, 314.31, 360.32, 373.66, 653.12	268.47
Buddleja Polystachya	238.64, 551.07	551.07
Canthuim oligocarpum	103.62, 282.60, 142.87, 153.03	103.62
Cassipourea malosana	188.40, 200.96, 280.25, 314, 360.32, 353.12	280.25
Diospyros abyssinica	150.72, 153.03, 175.84, 197.82, 200.96, 266.90, 268.47, 313.22, 314, 653.12	153.03
Discopodium eremanthum	117.75, 163.28, 164.85, 483.56	164.85
Dombeya torrida	373.66	373.66
Pittosporum viridiflorum	213.52	213.52

5.11 Probabilities of Self-replacement of Gap Makers and by Gap-filler Species

Only five of the fourteen gap maker species were found to exhibit self-replacing in the course of this study (Table 10). Whereas *Diospyros abyssinica* is recorded as the highest self-replacing (0.86) gap maker, low probabilities (< 0.50) of self-replacement characterize most of the gap makers. Furthermore, gap makers such as *Hagenia abyssinica, Hypericum revolutum, Schefflera abyssinica* and *Schefflera volkensii* lack regenerating individuals in the forest gaps. In Harena forest, most of the gap makers are being replaced by non -gap maker gap filling species such as *Brucea antidysenterica* and *Lepidotrichilia volkensii (*Table 10).

Table 10: The probabilities of the gap makers being replaced by themselves and gap-fillers species in Harena Afromontane forest (The probabilities of self-replacement are indicated in bold; dashes denote zero probabilities)

Gap-makers	**Gap-fillers**																				
	Ala	Bea	Crm	Dia	Dot	Erb	Gas	Hya	Hyr	Pra	Mym	Sha	Shv	Syg	Bra	Cao	Cam	Lev	Pof	Poa	Ved
Ala	-	0.07	-	0.07	-	-	0.02	-	-	-	-	-	-	-	0.23	-	0.08	0.33	-	-	0.17
Bea	-	**0.18**	-	0.24	-	-	-	-	-	-	-	-	-	-	-	0.18	-	0.24	-	-	0.18
Crm	0.05	0.08	-	0.03	-	-	0.02	-	-	0.04	-	-	-	-	0.35	0.03	0.01	0.14	-	-	0.21
Dia	-	0.14	-	**0.86**	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	-	-	-
Dot	-	0.19	-	0.09	-	-	0.02	-	-	-	0.13	-	-	-	0.44	-	0.02	0.07	-	-	-
Erb	-	0.1	-	0.02	-	-	-	-	-	-	-	-	-	-	0.29	-	-	0.47	0.03	-	0.13
Gas	-	0.47	-	-	0.03	-	-	-	-	-	0.02	-	-	-	0.41	-	-	0.03	-	-	0.03
Hya	-	0.08	-	-	-	-	0.02	-	-	-	-	-	-	-	0.45	-	0.04	0.26	-	-	0.39
Hyr	-	-	-	-	-	-	-	-	-	-	0.13	-	-	-	0.67	-	-	-	-	-	-
Pra	-	0.02	0.22	0.06	-	0.02	-	-	-	**0.26**	-	-	-	-	-	-	-	0.19	-	-	0.26
Mym	-	0.14	-	-	-	-	-	-	-	-	**0.43**	0.04	-	-	0.43	-	-	-	-	-	-
Sha	-	0.14	-	-	-	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	-	-
Shv	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.70	-	-	-	-	-	-
Syg	-	-	0.1	-	-	-	0.02	-	-	-	-	-	-	**0.02**	0.37	-	-	0.08	-	0.06	0.14
Total occupancy	1	11	2	7	1	1	5	-	-	2	5	1	-	1	11	2	4	10	1	1	8

Abbreviations*: Ala= Allophylus abyssinicus, Bea= Bersama abyssinica, Crm= Croton macrostachyus, Dia=Diospyors abyssinica ,Dot= Dombeya torrida, Erb= Erythrina brucei, Gas= Galiniera saxifraga, Hya=Hagenia abyssinica,Hyr= Hypericum revolutum, Pra= Prunus africana, Mym= Myrsine melanophloeos, Sha= Schefflera abyssinica, Shv=Schefflera volkensii, Syg= syzygium guineense, Bra= Brucea antidysenterica, Cao= Canthium oligocarpum, Cam= Cassipourea malosana, , Lev= Lepidotrichilia vockensii, ,Pof= Polycias fulva, Poa= Poutera adolfi-friederici, Ved= Vepris dainellii*

5. 12 Soil Seed Banks

5.12.1 Species composition and densities of soil seed banks

Whereas a total of 690 Seedlings have germinated from the soil samples collected from the forest gaps, 390 seedlings were recorded from the forest canopy. At the gap sites ,the seedlings belonged to 46 plant species and 26 flowering plant families, while, At the closed canopy sites, the seedlings belonged to 31 plant species and 17 flowering plant families (Appendix 2). In proportion, the herbaceous species constituted 89%, woody species accounted for 5.7% and climbing vine species contributed only 5.3%. The proportion for the closed canopy sites seedlings are 90.2% for herbaceous species and 4 .9% for each woody species and climbing vine species (Table 11).

The over all mean density of the seedlings at gap sites down to 9 cm depth of soil was 762 seedlings/m^2 (Appendix 2). The contribution of herbaceous, woody and climber seedlings to the over all mean densities of the gap sites were 89.2%, 5.5%and 5.3% respectively. The over all mean densities of seedlings for the closed canopy sites down to 9 cm depth was 377seedlings/ m^2. Of these, the contribution of herbaceous species, woody and climbers to the over all mean densities were 90.2%, 4.8% and 5% respectively.

Table 11: No of species and density of seedling of different life forms

Life forms	No of Species		Seedling density / m^2	
	Gaps	Canopy	Gaps	Canopy
Woody species	8	3	42	18
Herbs	36	26	680	340
Vines	2	2	40	19
Total	46	31	762	377

5.12.2 Vertical distribution of the soil seed banks

Depth Variation in soil seed banks was evident at both gap and closed canopy sites of the forest. In both cases, seedling densities decreased with increasing soil depth. In other words, soil depth was inversely related to soil seedling density (Fig. 11). The number of species in the three layers of soil showed decrement down the soil layers. In upper soil layer of the gap site, 46 species, in the middle layer 35 species and the third layer 19 species germinated. At the canopy sites 30, 20 and 10 species were germinated at the upper, middle and lower soil layers respectively (Fig. 12). As to woody species, the maximum number recorded was in the upper layer of soil seed bank. Twenty-seven and 12 seedlings of woody species germinated in the upper layers of the soil samples of the gaps and closed canopy sites respectively (Appendix 2).

5.12.3. Proportion of gap filling woody species recovered from soil seed bank

Out of the gap filling woody species recorded in the current study (Table 4), only 5 of them have been recovered from the soil seed bank samples in the forest gaps. These species were *Croton macrostachyus, Ficus sur, Prunus africana, Syzygium guineense* and *Vernonia amygdalina*. Noteworth is that *Croton macrostachyus* had the highest seedling density (8 seedlings /m^2).

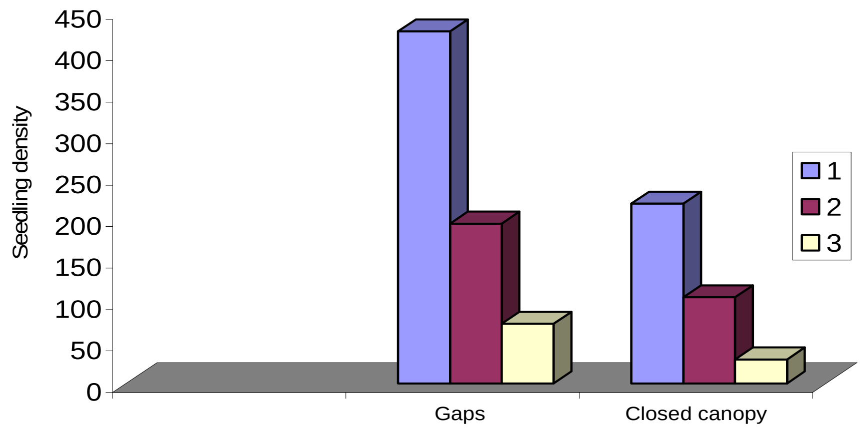

Fig.11: Density of seedlings /m^2 in soil seed banks in gaps and closed canopy sites

1 = 0 – 3 cm, 2 = 3 – 6 cm and 3 = 6 – 9 cm

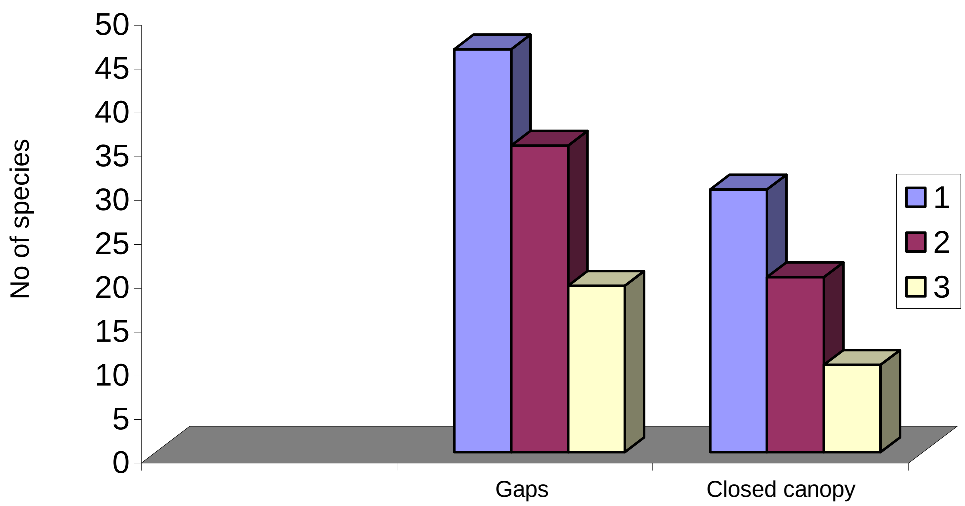

Fig. 12: No of species in soil seed banks of gaps and closed canopy sites

1=0-3 cm ,2=3-6cm ,3=6-9cm

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6. DISCUSSIONS

6.1 Tree Fall and Gap Characteristics

Tree fall gaps do contribute to important aspects of stand behavior. The disturbance regime of Harena forest was characterized by small gaps. The sizes of the expanded gaps, in turn, were characterized by small tree fall gaps. In Harena forest, 92.68% of the natural gaps were caused either through overthrow, snapping or branch breakage. This indicates that the main natural disturbance agent may be wind. Other disturbance agents such as insect and fungal attack, etc. may have minor contributions although it has not been dealt with in the current study. Roberts and Veblen (1993) have reported that most tree falls in Fuegian forest were reported to be the function of wind, i.e., uprooting and snapping.

Only, about 14.6% of the natural forest gaps of the studied area had an area of more than 400 m^2. Runkle (1982) has also found that small proportion of the gaps (4.7%) was characterized by an area of more than 400 m^2. No natural gap below 100 m^2 areas was encountered during this study since smaller gaps tend to fill very quickly than larger ones. In other words, one would more likely encounter larger gaps than smaller gaps because the former could be repeatedly disturbed by additional tree fallings. Young and Hubbell (1991) have reported that larger gaps were more significantly re-disturbed by secondary tree falls than were smaller groups in tropical forest sites. Cuevas (2003) has further noted a greater chance of getting larger forest gaps than smaller ones owing to the noted positive correlation between gap size and frequency of identifying them.

The Mean gap size (289.74 m^2) and range (101.03 - 896.93m^2) of Harena Afromontane forest were comparable to those reported for tropical forest gaps (range 140 - 628 m^2, Brokaw 1985) although they were found to be larger than those of Southern Cape forests of South Africa (20.5-37.7 m^2, Midgley *et al.*, 1995) and coastal Scrap forest of South Africa and (87-108 m^2, Obiri and Lawes, 2004).

The weak positive correlation between slope and gap size (r = 0.107) may generate an assumption that slope play limited roles in shaping forest gap size in the Harena Afromontane forest. Furthermore, the significant differences that exist between gap types may be attributed to the variations in sizes of the species involved in gap formation. For instance, most of the emergent trees and heavily crowned species such as *Dombeya torrida, Hagenia abyssinica, Croton macrostachyus, Allophylus abyssinicus, Prunus africana* and *Schefflera volkensii* formed gaps through overthrow resulting in relatively large forest gaps.

The current study has revealed that the mean DBH of the gap makers was 50 .4 cm (Table 2). Abayneh Derero *et al*. (2003) have reported that the mean DBH of the gap makers was >20 cm in Broad-leaved Afro-montane forest of southwest Ethiopia. The study of gap makers in Harena forest indicated that gap makers recorded resemble the dominant species of the vegetation at a specific elevation range of the forest (Lisanework Negatu and Mesfin Tadesse, 1989). In Harena forest, natural gaps aged <13 years have constituted 92.68% of the gaps surveyed perhaps indicating that older forest gaps were not easily identifiable.

6.2 Gap versus Forest Canopy Regeneration

The higher number of saplings and seedlings per hectare in forest gaps than forest canopy may suggest high degree of recruitment potentials of canopy trees in the forest gaps than under canopy. Out of the 24 gap filling species, seedlings and saplings of *Buddleja polystachya, Croton macrostachyus, Dombeya torrida, Ficus sur, Polyscias fulva* and *Syzygium guineense* are found in gaps but not in the under story of closed canopy forest. This may be that these species demand light for regeneration. Furthermore, *C. macrostachyus* is a forest weed (or a pioneer gap-filler), which always dominates open areas in the forest. Obiri and Lawes (2004) have also found that some pioneer species were restricted to gap environment in the coastal scrap forest of South Africa. Furthermore, in the Harena, gap micro-environment may have favored recruitment and establishment of *Prunus africana, Myrsine melanophiloeos, Bersama abyssinica, Galiniera saxifraga, Vernonia amygdalina, Brucea antidysenterica, Maytenus undata, Cassipourea malosana* and *Diospyros abyssinica* since their saplings were the most common ones in the forest gaps. Besides, saplings of 75% of the gap-filling species were recorded in both forest gap and canopy perhaps due to less preference of canopy conditions. Noteworthy is that Welden *et al*. (1991) have also found that

89.9% of the saplings of 106 gap-fillers on Baro Colorado Island have shown less preference of canopy conditions. Moreover, Abayneh Derero *et al*. (2003) have reported that saplings of 98% of the species studied were found in gaps and closed canopy exhibiting less preference to canopy conditions. This might be an indication why most of the species to be available over most of the different ranges of light.

6.3 Gap Regeneration, Gap Size and Selected Physical Parameters

The observed weak relationships between density of species in gaps and gap size may suggest that most gap occupants were already present before gap formation due to advance regeneration and an insignificant subsequent establishment had occurred after gap creation. In other words, shade tolerant seedlings that existed before gap formation or due to re-sprouts under a shady condition could rapidly fill well-lit gaps. It follows that out of the 24 gap-filling species recorded in the current study, saplings of 18 of them were both recorded in forest gaps and canopy. Besides, seedlings of 10 of these species were commonly encountered in both forest gaps and canopy.

Altitude and slope could also be cited as additional factors for weak relationships of gap size and density of gap-fillers. In Harena forest, the number of gap-filling species and density of their saplings were negatively correlated to altitude and slope. The negative correlation between altitude and species richness in forest gaps could be due to the impact of the former on the species diversity and density (Lisanework Negatu and Mesfin Tadesse, 1989) since an increasing altitude entails a decreasing trend of the richness and density of gap filling species. Similarly, the slope of forest gaps determines the speed of run-off and drainage, nutrient and water content of the soil (Lisanework Negatu and Mesfin Tadesse, 1989), which in turn limits the richness, and density of gap-fillers. Moreover, as noted from survivorship curves of selected gap filler species, the number of saplings decreases as height increases (Fig. 9), indicating greater mortality at earlier stages of growth. This mortality might be due to herbivores activities or inter specific and intra specific competition for space and resources.

In general, gap size is not the only factor determining regeneration in the forest gaps. Spatial location within a gap, gap shape, orientation, aspect and time of gap creation may have major influences on local regeneration (Brokaw and Busing 2000). Thus, both gap heterogeneity and predetermined nature of gap-filling and advanced regeneration could with regard to why gap size alone has a low explanatory power as predictor of post disturbance species composition in gaps.

6. 4. Gap Makers and Replacement Probabilities

In Harena Afromontane forest, no single species has displayed exact gap size specificity. Almost all the 24 gap-filing species encountered were located at most of the available gap size ranges in line with natural altitude ranges. There is no recognizable pattern of species composition across the gradients of gap sizes (Appendix 1). Brokaw and Busing (2000) and Obiri and Lawes (2004) have also reported the existence of no recognizable sequence of species across the gradients of gap sizes.

Self-replacement probabilities in Harena are remarkably weak. In many cases, the species of tree creating a gap seemed to influence the species composition of its likely successors (Runkle, 1981), which could be considered as a tendency to self-replacement. However, Runkle (1982) has found a reciprocal relationship between the saplings and gap-makers. Swaine and Hall (1998) also found that in many tropical forests, the larger canopy species do not regenerate in the same locations in which the adults occur. Furthermore, Obiri and Lawes (2004) found less probabilities of self-replacement in south scrap forest of South Africa.

The weak self-replacement probabilities of the Harena Afromontane forest may indicate the unpredictable species assemblages in the forest gaps. These assemblages were attributed to a chance effect of recruitment and/or dispersal limitation of species from the surrounding species pool (Hubbell *et al.*, 1999). Midgley *et al.* (1995) have also found that no correlation has existed between species composition and gap size and forest structure in sub tropical forest in South-Africa indicating a random recruitment in gaps as the function of and dominant pattern for the more common tree species.

6.5 Forest Gap and Canopy Soil Seed Bank and Gap-fillers

6.5.1 Comprehensive species composition and density of seeds in the soil

The soil seed bank from the forest gaps and canopy in Harena has exhibited a fairly considerable amount of buried viable seeds belonging to several gap-filling species. A number of studies have already indicated the importance of soil seed banks for restoration ecology in different forests of Ethiopia (Demel Teketay and Gransterom, 1995; Getachew Tesfaye ***et al.***; 2004).

The mean densities of seeds at the gaps (762 seeds/m^2) and forest canopy (377 seeds/m^2) were closer to that reported by Getachew Tesfaye *et al*. (2004) for unburned sites of the Harena Afromontane forest (622 ± 15 seeds/m^2). On the other hand, the results reveal lower seed density when compared to the four Afro- montane forests studied, namely, Menagasha (12,300 seeds/m^2), Munessa-Shashimane (13,700 seeds/m^2), Gara-Ades (20,100 seeds/m^2) and Wof-Washa (2,400 seeds/m^2) (Demel Teketay and Gransterom, 1995). The low seed density of Harena forest may be due to factors such as temporal and spatial heterogeneity of soil seed banks. The current method may also have contributed to the low seed density of the forest as well. Furthermore, differential litters layers of the forest gaps may have attributed to the low seed density.

The number of species in the soil seed banks of the gaps and canopy of Harena forest is within the range reported by Garwood (1989), i.e., 8-67. The total number of species recorded in the soil seed bank from forest gaps (46 species) and canopy (31 species) were higher than those reported for unburned sites of Harena forest by Getachew Tesfaye *et al*. (2004). However, the current results have shown low numbers when compared to the number of species recorded at Munessa-Shashimane (58 species),Gara-Ades (92 species),Menagasha (66 species) and Wof-Washa (62 species) (Demel and Gramsterom, 1995).

In terms of life forms, the soil seed bank of Harena forest was dominated by herbaceous species at forest gaps and canopy. The contribution of woody species in the soil seed bank was small at both sites perhaps due that herbaceous species could produce persistent seed banks. Unlike the herbaceous species, most woody species such as ***Pouteria adolfi-friederici*** do not accumulate seeds in the soil for long period of time. Rico-Gray and Garcia-Franco (1992) found that herbs were the most important life forms in the soil seed bank of tropical low land deciduous forest. Furthermore, Demel Teketay and Gransterom (1995) found small proportion of woody species in Munessa-Shashimane, Gara Ades, Menagasha and Wof- Washa forests soil seed bank. They found that herbaceous species were the most important life forms in the soil seed banks. On the contrary, Getachew Tesfaye *et al*. (2004) have reported that the woody species dominated the soil seed banks of the unburned sites of Harena forest.

6.5.2. Vertical distribution of soil seed bank

In the forest gaps and canopy, the distribution of soil seed bank was similar. Soil seed banks decrease with increasing soil depth (Fig. 11). Number of species also shows similar trend (Fig. 12). These patterns of soil seed banks distribution have been reported several times (Garwood, 1989; Demel Teketay and Gransterom, 1995; Getachew Tesfaye *et al*., 2004). The variations in seedling density and species richness between the gap and closed canopy sites might indicate that the majority of the species with permanent seed banks are gap colonizers. Demel Teketay and Gransterom (1995) have also reported that 58% of the species with persistent seed banks were gap colonizers.

6.5.3 Gap-filling woody species and soil seed bank

In Harena forest most of the gap-filling woody plant species failed to germinate from soil seed banks. Out of the gap-filling species (Table 4), only five of them have germinated from the soil seed banks. This could be due to that the majority of the canopy species of the forest do not have viable seeds in the soil seed bank. In other words, the rarity or the non-existence of the original gap-maker species could be due to the low availability of diaspores. It has been variously reported that diaspores availability is the function of the attainment of a climax-like floristic composition in gaps (Guevaro *et al*., 1986; Meclanahan, 1986; Purata, 1986; Rico-Gray and Garcia-Franco, 1992). Furthermore, some canopy species are known to possess recalcitrant seeds and adapted to germination more or less immediately after seed shed. For instance, Demel Teketay and Gransterom (1995) have found that *Bersama abyssinica* has recalcitrant seeds. Like wise, *Pouteria adolfi friederici* has seeds which even germinate in a couple of hours or only over night. Other canopy species may have the capacity to store their seeds in the soil for several years yet fail to germinate within a short period of green house germination trial.

Alternative explanation for the scarcity of gap-makers in the Harena may be predation, i.e., some species have a fast germinating seeds (e.g. *P. adolfi-friederici*) only to be cleared by wild animals immediately afterwards. In other words, predation may play an important role in reducing the seed population in the soil bank. Furthermore, foraging on fruits of e.g. *Syzygium guineense* and *Ficus* sur by wild animals such as monkeys and birds may deposit the diaspores at unsuitable sites away from the forest gaps. Johnson (1975) has reported seed predation as one cause for a decrease in buried seed survival with age of vegetation. According to Lavarel *et al*. (1991), various biotic and a biotic factors interfere with the initial seed distribution after seed dispersal such as seed predation. At the same time, predation pressure has been thought to be high for tropical fruits (Howe *et al.*, 1985; Schupps, 1990; Tanaka, 1995). Generally, pre-dispersal and post dispersal predation effects are known to affect seed dynamics. In general, soil seed banks of the forest gaps do not contribute much to the composition of gap-filling woody species at Harena forest owing to the aforementioned complex yet interconnected biological and environmental factors.

7 CONCLUSION AND RECOMMENDATIONS

The investigation of gap dynamics in Harena forest revealed that small scale disturbances caused by single tree or group of trees fall are essential for maintaining the diversity of woody species in the forest .In addition to this, the mode of mortality is mainly related to the species of canopy tree that involved in the process.

The variations observed in the gap sizes were due to various factors such as altitude, slope and size of the tree that made the gap, that is gap sizes differed based on mode of disturbances.

Even though, gap size plays an important role in determining species richness in forest structure, the effect of gap size on species richness and sapling density of Harena forest is low. Beside this fact, the gap environment is more favorable for the recruitment of most of the woody species than the closed canopied sites.

Self-replacement probabilities in the forest are low. This indicates that the loss of important canopy trees such as, for example, ***Hagenia abyssinica*** would result in loss of genetic diversity and imbalance of ecosystem functioning.

Investigation of the soil seed banks of Harena forest revealed that the recovery of most of woody species from soil seed banks is very low. Therefore, if the present vegetation degradation continues, as observed from the current actions of the settlers in the forest, the recovery of it, through succession would require a long period of time.

The study of gap dynamics was not carried out in this moist afro- montane forest before. Therefore, the current study of gap dynamics could provide some aspects of gap regeneration in the forest. This could attract various professionals to carry out further assessments on different aspects of gap dynamics of the forest. Therefore, I recommended that:

- Ecologists, biologists and other related professionals should pay attention to the study of gap dynamics, as it is important in maintaining the diversity of species and stability of ecosystems

- Illegal logging of forest trees, especially, the indigenous ones, by the settlers for timber and even large scale logging by the government institutions should be stopped or if not possible should be minimized;

- Part of Harena forest is located in the Bale National park. Further more, it is one of the largest remaining scraps in maintaining the climatic conditions of the country. It is also an area that is rich in biodiversity. As a matter of these, the government and the people should take unreserved involvement in conserving the vegetation of the area. In this respect, the involvement of the resource users (the local people) should be enhanced, by making them aware of the importance of conservation and take care of the resources. Lastly, if possible, the remaining part of the forest should as far as possible be included in the Bale National park.

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Appendix1: Variables measured for 41 natural gaps in Harena forest

Plot No	Altitude (masl)	Slope(%)	Gap orientation	Gap age	Gap size m^2	Number of G.F.Species	No of Saplings	No of gap fillers
1	3000	10	NW	10	164.85	2	2	2
2	2975	20	NW	9	117.75	2	3	3
3	2950	5	SE	12	141.3	1	2	1
4	2925	25	NE	7	213.52	2	4	2
5	2900	30	SE	8	163.28	4	6	6
6	2875	30	SE	13	282.6	3	8	7
7	2850	15	SW	10	483.56	5	7	5
8	2825	30	SE	7	266.9	3	9	7
9	2800	20	SW	15	428/61	2	20	20
10	2775	25	SE	4	238.64	2	5	2
11	2750	10	SW	10	370.91	3	15	10
12	2725	10.5	SW	9	685.71	1	24	20
13	2700	10	SE	7	333.86	1	9	9
14	2675	15	SE	10	896.93	3	30	23
15	2650	20	ME	8	313.22	2	10	8
16	2625	30	SW	2	238.64	3	10	7
17	2600	10	ME	3	276.32	4	27	17
18	2575	10	SW	10	551.07	3	21	19
19	2550	25	SW	3	219.8	3	13	11
20	2525	15	SW	6	314	7	12	11
21	2500	10	SE	12	312.22	3	15	14
22	2475	17.5	SW	3	150.72	2	8	7
23	2450	5	SE	5	266.9	4	14	14
24	2425	10	SE	4	373.66	3	23	18
25	2400	10	SE	5	268.47	6	29	11
26	2375	20	SE	4	653.12	5	24	16
27	2350	25	SE	5	280.15	6	15	6
28	2325	10	SE	7	360.32	5	13	9
29	2300	5	SE	10	200.96	10	26	20
30	2275	5	SE	4	268.47	6	62	35
31	2250	10	SE	10	188.4	4	18	17
32	2225	5	SE	3	188.4	7	24	17
33	2200	5	SW	3	103.62	7	26	17
34	2175	0	SW	5	282.6	8	60	42
35	2150	5	E	10	142.87	10	25	17
36	2125	5	SW	4	314.31	8	34	8
37	2100	5	NE	6	197.82	9	28	19
38	2075	5	SW	2	175.84	7	18	10
39	2050	5	SW	13	153.08	5	49	35
40	2025	5	SE	12	101.03	4	23	23
41	2000	5	SE	8	196.97	6	34	30

Species	Family	Gap sites A	B	C	Den.N=41	Closed Canopy site A	B	C	Den. N=41
1. Woody speices									
Croton macrostachyus	Euphorbiaceae	5	2	0	8	3	2	0	5
Ficus sur	Moraceae	1	1	0	2	0	0	0	0
Hypericum quartinianum	Hypericaceae	2	1	0	3	1	0	0	1
Prunus africana	Rosaceae	2	0	0	2	0	0	0	0
Syzyguim guineensee	Mytraceae	1	0	0	1	0	0	0	0
Vernonia amygdalina	Asteraceae	3	0	0	3	0	0	0	0
Rubus volkensii	Rosaceae	12	5	2	23	8	2	1	12
Acanthus eminens	Acanthaceae	1	1	0	2		0	0	0
		27	**10**	**2**	**42**	**12**	**4**	**1**	**18**
2. Hebaceous species									
Acmella cavlirhiza	Asteraceae	2	1	0	3	0	0	0	0
Achrynthes aspera	Amaranthaceae	1	0	0	1	0	0	0	0
Alchemilla abyssinica	Rosaceae	10	5	3	20	10	4	2	17
Amaranthus graecizans	Amaranthaceae	2	1	1	4	0	0	0	0
Ardisiandra wettsteinii	Pramulaceae	9	1	0	11	8	1	0	10
Cardamine africana	Brassicaceae	4	0	0	4	0	0	0	0
Cerastium octandrum	Caryophyllaceae	1	1	0	2	0	0	0	0
Conyza nana	Asteraceae	8	2	1	12	4	3	1	9
Crassula alsinoides	Crassulaceae	82	34	10	137	22	17	3	47
Crotalaria agatiflora	Fabaceae	8	7	3	20	4	1	1	7

Cynoglassum densifoliatum	Boraginaceae	2	0	0	2	1	0	0	1
Cyperus richardii	Cyperaceae	3	2	1	7	2	1	0	3
Cyperus rigidifolius	Cyperaceae	3	2	1	7	2	2	0	4
Dichrpcephala chrysanthemifolia	Asteraceae	8	2	1	12	30	1	1	5
Droguetia iners	Urticaceae	12	5	3	22	6	3	0	5
Eragrostis schweinfruthii	Poaceae	4	3	0	8	3	0	0	3
Helichrysum Cymossum	Asteraceae	3	1	1	5	0	0	0	0
Hibiscus ludwigii	Malvaceae	94	33	21	160	58	28	11	105
Hibiscus surattensis	Malvaceae	3	2	0	5	3	2	0	5
Impatiens rothii	Balsaminaceae	4	2	0	7	2	1	0	3
Isolepsis fluitans	Cyperaceae	11	9	3	25	5	4	0	10
Isolepsis setacea	Cyperaceae	5	4	1	11	0	0	0	0
Kalanchoe petitiana	Crassulaceae	5	1	0	7	5	0	0	5
Lactuca olracea	Brassicaceae	1	0	0	1	2	0	0	2
Laggera alata	Asteraceae	9	5	0	15	10	6	0	17
Oxalis procumbens	Oxalidaceae	44	20	7	77	23	13	6	46
Phyllanthus oblongiglans	Euphorbiaceae	1	0	0	1	7	3	1	12
Plantago africana	Plantagonaceae	1	0	0	1	0	1	0	1
Senecio steudelii	Asteraceae	9	1	1	12	7	0	0	8
solanum nigrum	Solanaceae	13	10	3	28	5	2	1	9
Solanum sp	Solanaceae	6	4	2	13	3	0	0	3
Sonchius asper	Asteraceae	4	4	1	10	1	0	0	1
Stellaria media	Caryophyllaceae	1	1	1	3	2	1	3	3
Thymus schemperi	Laminaceae	1	0	0	1	0	0	0	0
Veronica simensis	Scrophulariaceae	7	4	3	15	1	0	0	1
Veronica glandulosa	Scrophulariaceae	5	3	0	9	2	1	0	3
		379	**168**	**67**	**680**	**195**	**94**	**27**	**340**
3. Climbers (Vines)									
Ipoema ericarpa	Convolvulaceae	17	14	3	37	6	3	0	10
Zeheria scarpa	Cucurbitaceae	2	1	0	3	4	3	1	9
		19	**15**	**3**	**40**	**10**	**6**	**1**	**19**
Total		**425**	**193**	**72**	**762**	**217**	**104**	**29**	**377**

Appendix 2:Number of seedlings and respective soil seed densities /m^2 for species that germinated in different soil layers of samples collected from the gaps and closed canopy sites of Harena forest. Soil layers A=0-3cm, B=3-6cm And C=6-9cm